TAXONOMY, PHYLOGENY, AND VARIABILITY OF *PSEUDISOGRAPTUS* BEAVIS

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ABSTRACT. Manubriate isograptids from the Castlemainian and Yapeenian (Arenig) of New Zealand, Australian, and Chinese collections are described and analysed in terms of population systematics. *Pseudisograptus manubriatus* (T. S. Hall, 1914) is divided into five subspecies, of which *P. m. koi*, *P. m. harrisi*, *P. m. janus*, and *P. m. texanus* are new; *P. bellulus* sp. nov. and five other *Pseudisograptus* species are described. A tentative phylogenetic scheme is constructed from their stratigraphic occurrence and a cladogram of pseudisograptids and other forms with manubriate features. Similarities in proximal structure and thecal form link the pseudisograptids with the glossograptids, and the monophyletic suborder Glossograptina Jaanusson, here taken to include *Apiograptus* (syn. *Exigraptus*), *Kalpinograptus* (syn. *Apoglossograptus*), and *Pseudisograptus*, is down graded to family rank. The paraphyletic *Pseudisograptus* is a sister group to the monophyletic subfamily Glossograptinae.

Details of proximal development and structure of the manubrium are described for *P. m. janus* and *P. bellulus*, using pyritized specimens preserved in full relief. From this data and that gleaned from flattened specimens of other taxa it is concluded that the manubrium structure described by Bulman, and taken to be a paradigm for the group, is in fact rare and atypical.

PSEUDISOGRAPTUS MANUBRIATUS is an extraordinary species, even among isograptids, for its wide range of morphologic variation. Previous workers have referred to or described this variation (Hall 1914; Harris 1933; Cooper 1973, 1979; Cooper and McLaurin 1974) and four informal forms were erected by Cooper and McLaurin (Forms A–D) who remarked (p. 78): 'although [the forms] are linked by intermediates and are unlikely to prove to be distinct taxa, they do appear to represent end points along different lines of variation'. In this study we approach the problem from the point of view of population systematics and revise the entire group of manubriate isograptids, here referred to as the manubriate complex. The group is united by possession of a manubrium. The study is based on the original collections from New Zealand of Cooper (1973; with locality details), supplemented in all cases by additional material; collections from Willey's Quarry, Macedon, Victoria, made by several workers; and new material from Zhejiang Province in China, including pyritized specimens in full relief which allows proximal development and structure of the manubrium to be described in detail and analysed.

The stratigraphic ranges of the taxa discussed are shown in text-fig. 4. The ranges of British species within the *Isograptus caduceus gibberulus* Zone (as redefined by Jenkins 1982) is unknown (Jenkins 1982, p. 240), and their range is shown throughout the interval correlated with that zone (upper Castlemainian to lower Yapeenian). The earliest form, *P. hastatus*, appears in the lower part (*I. victoriae maximus*) of the Castlemainian Ca3 zone of Australasia. The main radiation took place in the early Yapeenian and by the end of the Yapeenian all pseudisograptids had disappeared.

Geographically the group is rather less widespread than isograptids of the *victoriae* and *caduceus* groups. Apart from the Australian, Texan, and Chinese species discussed herein, the group is represented in Alaska (*P. gracilis*; Carter and Tailleur 1984, fig. 6) and the Basin Ranges, USA (*P. dumosus*; listed by Ross and Berry 1963, p. 94), and Kazakhstan (Tsai 1974 lists forms here attributed to *P. manubriatus koi* and *P. dumosus*). *Kalpinograptus* is known from NW China (Xinjiang; Jiao 1977) and Alabama (Finney 1978 as *Apoglossograptus*), and *Apiograptus* is known from Sweden (Cooper and Lindholm 1984). The glossograptids are world-wide.

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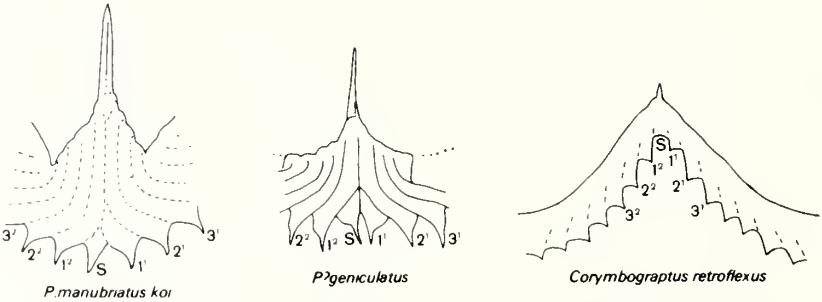
MANUBRIATE MORPHOLOGY, VARIATION, AND ANALYSIS

A feature of all isograptid populations described to date is the wide range of intraspecific morphologic variation (Cooper 1973; Cooper and Fortey 1982). Failure to appreciate this wide range can lead to invalid splitting of taxa (Beavis and Beavis 1974). The range of morphologic variation displayed by the manubriate species, however, and particularly *P. manubriatus*, is exceptionally great. It is more important than ever to adequately describe the variation and adopt a population approach to the systematics of the group. We have used statistical analysis of measurable characters to describe this variation quantitatively and discuss below the measured characters and techniques used. The most useful features for taxonomic purposes relate to the proximal portion of the rhabdosome (Cooper and Fortey 1982, 1983) and we have therefore concentrated on this region.

The manubrium

The term *manubrium* has come into general use for the structure produced by the initial downward growth of proximal thecae prior to the upward flexure of stipes in isograptids. Because it is regarded as apomorphous (a defining character) for the manubriate complex and because its size and shape have been found to be useful in discriminating taxa it is here defined with more precision than in the past. It is comprised of the proximal portions of initially downward growing thecae (th1^2 and beyond). Its base is taken at the level of the sharp upward flexure in the dorsal stipe margin (text-fig. 2A) at the point of origin of the third or later thecal pair. Beyond this point the two thecal series grow independently outward and upward as the stipes proper. The structure of the manubrium is known from three species preserved in relief: *P. bellulus* sp. nov., *P. manubriatus texanus* ssp. nov., and *P. m. janus* ssp. nov.



TEXT-FIG. 1. Manubrium development in *Pseudisograptus manubriatus koi* (strongly developed) and *P.? geniculatus* (weakly developed). *Corymbograptus retroflexus* is shown for comparison, with initially downward growing stipes which do not form a manubrium.

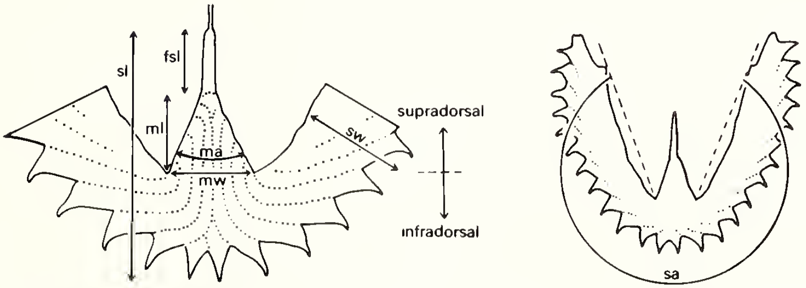
The manubrium results from a lengthening of the sicula and proximal thecae and delay in point of upward flexure of the dorsal stipe margins, together with a concentration of thecal origins. It is distinguished from analogous (*not* homologous) structures in other didymograptids in which downward initial growth of stipes is not accompanied by elongation of proximal thecae and the rhabdosome has a proximally concave ventral outline (text-fig. 1).

In all manubriate species for which data are available the growth paths of the sicula and first theca overlap each other in mid-length, as seen in bilateral view, but recurve so that their apertural regions are directed away from each other. This curved growth path is followed and often accentuated by subsequent thecae. The alternate superposition of one theca on another in the two thecal series results in a plaited arrangement of proximal thecae—clearly illustrated by Bulman (1968, fig. 1) and reaching its most elaborate state in *P. m. janus* where the first five thecae are plaited (text-fig. 18). The extensive overlap of one thecal series on the other, illustrated by Bulman in the specimen from Texas (*P. m. texas*) and for a time taken as a paradigm for the group (Beavis 1972; Cooper and McLaurin 1974) is now known to be rare; with the exception of *Kalpinograptus*, there is generally no overlap in specimens other than that from Texas.

Development of the manubrium takes place entirely on the reverse side of the rhabdosome and the two sides (obverse and reverse) can appear very different, as in *P. m. janus*. Other features of the manubrium, such as the left- or right-hand origin of thecae and the tendency for the stipe dorsal margin to grow around in a loop at the point of flexure, are discussed with the species concerned.

Morphologic terms

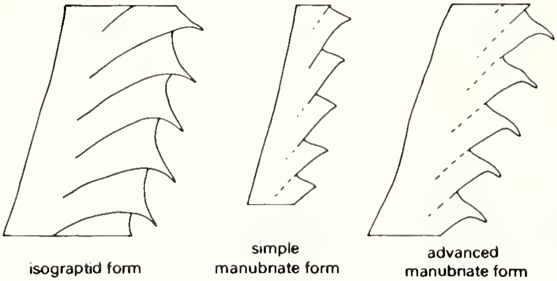
Rhabdosome characters referred to in the descriptions below are shown in text-fig. 2. *Sicula length*, *proximal stipe width*, *distal stipe width* are in general use and need no explanation. The *manubrium* is that structure involving the proximal portions of th1^2, 2^1, and all subsequent thecae with initially downward growth; *width* and *length* (= height) *of the manubrium* are measured as indicated. The *free proximal length* of the sicula is measured from the apex to the top of the manubrium. In most manubriate species the sicula passes apically into a stout nema and the apex of the sicula is sometimes difficult to determine. From the few well-preserved specimens available the apex of the sicula passes via a slight constriction into the nema and this constriction is generally visible even in fully flattened specimens. The possible margin of error in determining the apex of the sicula is only a small proportion (about 5 %) of total sicula length but is a considerable portion (about 20 %) of the free proximal sicula length. For this reason, free proximal sicula length was not used for multivariate analysis.



TEXT-FIG. 2. Terms and measured characters used in the descriptions: fsl, free proximal portion of the sicula; sl, sicula length; ml, manubrium length; mw, manubrium width; ma, manubrium angle; sw, stipe width; sa, stipe divergence angle.

The *manubrium angle* is the angle subtended by the *manubrium shoulders*. *Stipe divergence angle* is the ventral (external) angle measured between the chords joining the distal extremity with the point of proximal flexure (i.e. base of manubrium shoulder) in the dorsal stipe margin. The term *supradorsal* is used as defined by Cooper (1973) to refer to that portion of the sicula and proximal thecae lying above the point of flexure in the dorsal stipe margins. The term *infradorsal* is introduced here to refer to that portion below the point of flexure.

The term *advanced manubriate thecal form* (text-fig. 3) refers to the outline form of thecae, particularly in the distal part of the rhabdosome, characteristic of *Apiograptus* and the *P. manubriatus*–*P. tau* group and, of course, of the glossograptid—*Kalpinograptus* group. Apertural margins are extended into an outwardly directed ventral process in the manubriate species, homologous with the apertural spine in glossograptids. The apertural margin is inclined to the stipe axis at a high angle and is undulating, suggesting the presence of lateral lappets as described by Skevington in isolated material of *P.*? *geniculatus*. Thecal ontogeny in glossograptids has been discussed by Finney (1978). The term *simple manubriate thecal form* refers to thecal outline form in the *P. dumosus–P. gracilis* group and in *P. hastatus*. Distal thecae are relatively straight and apertural margins are highly inclined but lack a ventral process or suggestion of lateral lappets.



TEXT-FIG. 3. Thecal form: simple manubriate (*Pseudisograptus gracilis*), and advanced manubriate (*P. manubriatus koi*) thecal form contrasted with isograptid thecal form (*Isograptus victoriae victoriae*).

Thecal spacing was found to be difficult to measure precisely in rhabdosomes with curved stipes and to show relatively little variation where it could be measured; it is therefore not used in the statistical analysis. Thecal inclination similarly can seldom be measured in any precise way in flattened rhabdosomes and is also not used in analysis.

Isograptid symmetry was defined by Cooper and Fortey (1982) for rhabdosomes with the sicula and first theca symmetrically disposed on either side of the rhabdosome midline. The term *maeandrograptid symmetry* is used here for rhabdosomes which, in contrast, have the rhabdosome midline passing through the sicula and th1^1 and 1^2 arranged more or less symmetrically on either side, as exemplified by *Maeandrograptus schmalenseei*.

The terms obverse and reverse need clarification when being used for pericalycal rhabdosomes (Bulman 1968, p. 214). As used here *reverse* refers to that side of the rhabdosome on which th1^2 grows across the sicula in its *early* development from th1^1. In pericalycal forms such as *Cryptograptus* (Bulman 1970, fig. 62.3) the distal growth path of th1^2 may recross the sicula on the obverse side. On the *obverse* side of the rhabdosome the sicula is not obscured by the 'crossing canals'.

The terms pericalycal and platycalycal also need clarification. *Pericalycal*, as defined by Bulman (1970, p. V10), refers to 'mode of development of scandent (monopleural) rhabdosomes associated with dicalycal th1^1 and left-handed origin of th1^2, sicula becoming largely enclosed on both sides during subsequent development'. Emphasis was laid by Bulman (1968) on two features: first, th1^2 grows sinistrally, its distal portion (in *Cryptograptus*) wrapping around the *obverse* side of the sicula opposite to that of th1^1; secondly, development is of artus type (th1^1 dicalycal) enabling (or causing) the two thecal series to develop on opposite sides of the sicula and thereby envelop it. In contrast *platycalycal* development refers to the 'normal' development mode in which all proximal budding takes place on the reverse side of the rhabdosome, leaving the sicula free on the obverse side, e.g. *Glyptograptus*, *Isograptus*, etc. The distinction becomes blurred in such monopleural rhabdosomes as *Cryptograptus marcidus* and *Glossograptus ciliatus*, both described from isolated growth stages by Finney (1978), in which development is of 'normal' isograptid type (th1^2 dicalycal) but the sicula becomes enveloped by the two thecal series from the second or third thecal pair onwards. Should precedence be given to a development of sinistral mode and *artus* type, or to the envelopment of the sicula? Bulman appears not to have regarded envelopment of the sicula as of over-riding importance because he comments (1968, p. 214) that *P. manubriatus* from Texas 'is fundamentally platycalycal, though it simulates the pericalycal type to some extent in that the proximal portions of th4^1 to th6^1 seem to originate on the obverse side of the rhabdosome and possibly enclose or cover some portion of the sicula. This is probably induced by the semicircular course of th2^2 and does not constitute a true transition between the two types.' The proximal structure of Finney's species can be regarded as a more extreme expression of this feature (discussed in detail herein), and therefore would not have been regarded by Bulman as 'truly' pericalycal. In this discussion we use the term *pseudopericalycal* for forms in which the sicula is enveloped by the developing thecal series but in which development is of 'normal' isograptid type and dextral; it is known in *C. marcidus*, *G. ciliatus*, and probably in *Kalpinograptus*, and is incipiently developed in the Texan *P. manubriatus*. Pericalycal development has been described in *C. tricornis* (Bulman 1945) and in *G. holmi*, *Paraglossograptus*? sp., and *Skiagraptus* sp. (= *Bergstroemograptus crawfordi* (Harris) of Finney and Chen 1984), all described by Whittington and Rickards (1969). However, strict definition of the term pericalycal must await resolution of the problem raised by Finney's (1978) reinterpretation of the proximal development of *C. tricornis* and *G. holmi*.

Measured characters

To quantitatively describe morphologic variation the characters listed below were used. They are readily measured and assumed to have undergone either no change, or standard change from specimen to specimen, on flattening.

Sicular length, with a possible 5 % error in determining the apex (mentioned above). *Free proximal sicula length*, with a possible 20 % error (mentioned above); this feature must be used with caution but it is nevertheless a conspicuous and distinctive feature of the rhabdosome in all species. *Infradorsal sicula length* gives a measure of the proximal 'depth' of the rhabdosome. However, it is merely sicula length from which has been subracted the manubrium length plus the free proximal sicula length; it is therefore totally dependent on the other two characters and is not used with them in multivariate analysis. *Manubrium height*: because of the tendency in rhabdosomes with highly divergent stipes for the dorsal stipe margin to grow around in a loop and overlap the base of the manubrium, the point of intersection between the manubrium shoulders and the dorsal stipe margin, taken as the base of the manubrium, may not in fact be the true base of the manubrium as revealed in growth stages. The true manubrium length in *Pseudisograptus manubriatus koi* 'form D' is therefore likely to be a little greater than measured in mature rhabdosomes. *Manubrium width*: as with manubrium length, true manubrium width in *P. m. koi* 'form D' is likely to be greater than measured. *Manubrium angle*: variation in this feature has been noted by most previous workers; it is very largely a consequence of manubrium length and width and is not therefore used with them in multivariate analysis. *Proximal stipe width* is measured immediately after the initial flexure of stipes. *Distal stipe width* is measured in the distal region of mature rhabdosomes, but proximal to the still-growing distal extremity. *Stipe divergence angle*: by convention this is measured ventrally (externally), so the wide variation seen in some species, such as *P. m. koi* (80°), is only a small proportion of the total divergence angle (280–360°). Thus the coefficient of variation for this character is misleadingly low (7) since it is inconceivable that a specimen with stipes diverging at less than 180° would still be called an isograptid; a more appropriate value (60) is achieved by measuring the included angle (0–80°). It should be noted that the high coefficients quoted by Cooper (1973) were inadvertently arrived at by measuring the included angle, although the actual divergence angle was given as an excluded (ventral) angle.

Rhabdosome astogeny and allometry

The change in rhabdosome proportions with astogeny (heterauxesis) in isograptids was discussed by Cooper (1973, pp. 92–94). The rhabdosome grows by terminal addition of thecae. Cooper inferred from growth stages that only the three to six most recently formed thecae at the growing (distal) end of the stipe had not reached their full length and should be regarded as immature. Older thecae preceding the distal six had completed their growth and measurements based on them are free of the effects of astogeny.

We now have quantitative evidence supporting this inference. If any of the measured features continued to grow throughout growth of the rhabdosome they should show a significant positive correlation with stipe length which, up to the genetically determined maximum, changes continuously by the distal addition of new thecae, and is the main contributor to allometric change.

The correlation of stipe length with other measured characters in six pseudisograptid taxa is given in Table 1. The only significant positive values are with proximal stipe width (in *P. dumosus*) and sicula length (in *P. m. manubriatus* and *P. m. harrisi*); most values are low or even negative. Certainly there is no consistent pattern which one would expect if either sicula length or stipe width increased throughout growth of the rhabdosome. *P. m. manubriatus* and *P. dumosus* are represented by small populations and we suspect that these values, like the negative values for stipe width and manubrium length in *P. m. koi*, and for manubrium width (which cannot change with growth) in *P. gracilis* are due to chance. We therefore feel confident that the measured characters reflect mature rhabdosome dimensions and are free from allometric effects.

TABLE 1. Correlation of stipe length with sicula length, manubrium width, manubrium length, and proximal stipe width in six pseudisograptids. Values significant at the 95 % level are in italics

	N	Sicula length	Manubrium width	Manubrium length	Proximal stipe width
P. hastatus (T. S. Hall)	22	0·269	0·156	0·182	0·224
P. gracilis (Ruedemann)	18	−0·223	*−0·442*	−0·079	−0·151
P. dumosus (Harris)	22	0·258	0·242	0·043	*0·562*
P. m. manubriatus (T. S. Hall)	13	*0·640*	−0·046	−0·050	0·382
P. m. koi ssp. nov.	50	−0·058	−0·008	*−0·273*	*−0·290*
P. m. harrisi ssp. nov.	30	*0·391*	0·306	0·052	−0·059

Statistical methods

The basic univariate statistics for each character—minimum and maximum values, mean, standard deviation, and coefficient of variation are given in the appendix. Frequency distribution histograms depict the variation for each character and provide the simplest test of whether or not a sample represents a single population. Histograms of sicula length and manubrium size (text-fig. 14A, C) measured on specimens from Jimmy Creek, for example, suggest that two populations are represented (*P. m. koi* and *P. m. janus*). Character correlation matrices are given in the appendix and bivariate plots of selected characters are shown in text-figs. 15, 24, and 28. The bivariate plots provide a convenient way of discriminating taxa in the *hastatus* and *dumosus* groups (text-figs. 24, 28).

A more comprehensive way of showing the distribution of specimens throughout a population in terms of their total morphologic variation is multivariate principal components analysis (PCA), which uses all measurements on all specimens (complete data sets only). Because the variates (character states or measurements) have various scales (e.g. stipe divergence ranges from about 270° to 360° whereas manubrium width ranges from about 0·7 to about 2·5 mm) the analysis was based on the correlation matrix rather than the dispersion matrix.

The two major axes generally together account for about 70 % or more of the total variance in the taxa studied by this method (*P. manubriatus* group, *P. gracilis*, *P. hastatus*, *P. dumosus*, and *P. jiangxiensis*) and lower order axes have therefore not been used. A plot of the principal components gives a more representative idea of the distribution of specimens in terms of the total morphologic variation than any univariate or bivariate plot, and often reveals clustering. Two groups are clearly distinguished in plots of *manubriatus*-like specimens from Jimmy Creek (*P. m. koi* and *P. m. janus*; text-fig. 6) and groups can be similarly recognized in plots of the *P. dumosus* and *P. hastatus* groups (text-figs. 25, 29). PCA is thus useful for taxonomic discrimination. Measurements on a single character in different populations may overlap in range, producing a single unimodal curve and giving the false impression of a single population; multivariate analysis helps reveal populations and identifies the characters most useful in discriminating them.

Only five of the measured characters have been used in PCA—sicula length, manubrium width, manubrium length, proximal stipe width, and stipe divergence angle (except for *P. dumosus* where rhabdosome width, measured at the level of the base of the manubrium, was used instead). Free proximal sicula length and manubrium angle are not used for reasons explained above, and infradorsal sicula length is not used with manubrium length because together they become highly dependent on sicula length. Distal stipe width also will obviously be highly dependent on proximal stipe width and is omitted. All characters are equally weighted.

In view of the phylogenetic approach to taxonomy and classification advocated below it should be noted that PCA is basically phenetic, i.e. there is no distinction between primitive (plesiomorphic) and derived (apomorphic) characters. The distribution of specimens depends on their overall morphology as represented by the measured characters, whereas in the evolutionary and phylogenetic (cladist) methods emphasis is placed on selected 'key' (apomorphic) characters (see discussion below). PCA is used here, however, only at the level of distinguishing population (species or subspecies) pairs and not for dealing with large groups of taxa, for which purpose there are better techniques available. Primitive characters will tend to falsely enhance the similarity among specimens seen by PCA, thereby reducing the discriminatory power of the method, unless there is a simultaneous secondary loss of two or more primitive characters in the one set of specimens that is *not* taxonomically significant but due to chance (sampling) or environmental factors, etc.; PCA would regard this as significant and group the specimens accordingly. All characters used herein are continuous variates and such a situation is most unlikely to arise.

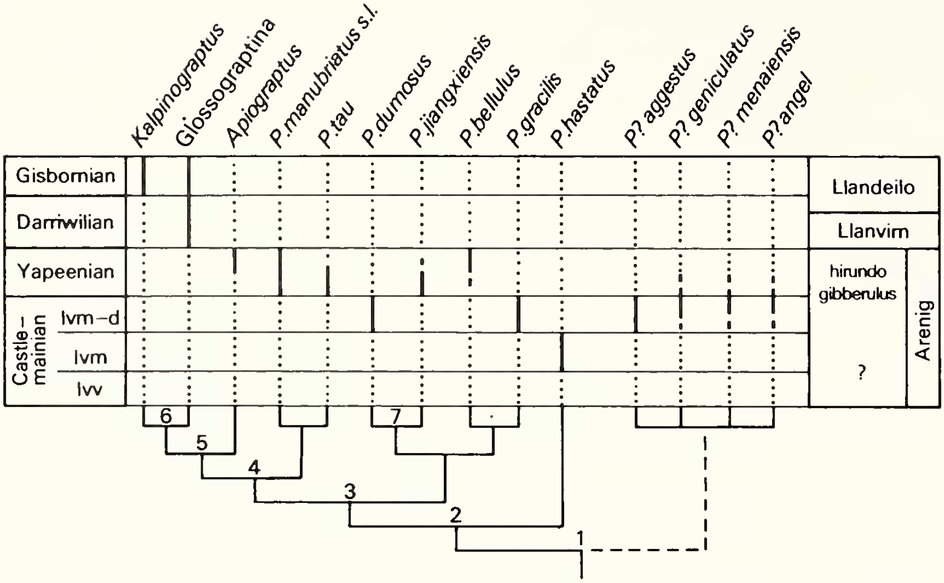
To obtain a measure of the degree of overlap between populations in multidimensional space a GENSTAT non-hierarchial classification program was used. This reclassifies specimens to that class ('taxon') in which they fit best. It does so by attempting to maximize the total of the Mahalanobis D^2 distances between classes. A population with a considerable morphologic overlap on a second population will have a relatively high percentage of its members reclassified into the second population. Thus a multivariate estimate of the percentage overlap between populations is obtained. This helps in deciding whether or not two populations are sufficiently distinct to separate as different subspecies or species, and to which of two species an odd, morphologically intermediate specimen should be referred. It is therefore particularly useful in the study of high variance populations such as the manubriate isograptids.

RELATIONSHIPS, PHYLOGENY, AND CLASSIFICATION

Relationships

From the following descriptions and discussion a tentative cladogram, showing the inferred relationships between taxa, can be constructed (text-fig. 4). Synapomorphies (shared derived characters) are specified in the caption.

The entire group is characterized by the possession of a manubrium. Those species with a weakly developed manubrium (*P.? geniculatus*, *P.? aggestus*, *P.? menaiensis*, and *P.? angel*) are only tentatively included, as a discrete sub-group. Of forms with a well-developed manubrium, *P. hastatus* alone lacks marked outward deflection of proximal thecae and has distal thecae which differ little from those of *Isograptus*; it is thus an isograptid of *I. victoriae* type with a manubrium suggesting that the *I. victoriae* group is the outgroup for comparison with pseudisograptids. The remaining pseudisograptids can be split into those with advanced manubriate thecal form and those with (primitive) simple manubriate thecal form. In the first category, one group includes *Kalpinograptus* (= *Apoglossograptus*) and the Glossograptina which share a fully developed pseudopericalycal proximal structure, and *Apiograptus* which has only a partially developed pseudopericalycal structure. If this grouping is correct, then scandency has either evolved independently in *Apiograptus*



TEXT-FIG. 4. Stratigraphic ranges of pseudisograptid and related taxa and a cladogram showing relationships between taxa. Shared derived characters (synapomorphies) specified by numbers: 1, presence of manubrium; 2, manubrium well developed; 3, strong outward deflection of proximal thecae, plaiting of proximal thecae, and simple manubriate form; 4, advanced manubriate thecal form; 5, pseudopericalycal structure partially developed; 6, pseudopericalycal structure fully developed; 7, expanded manubrium and shortened stipes.

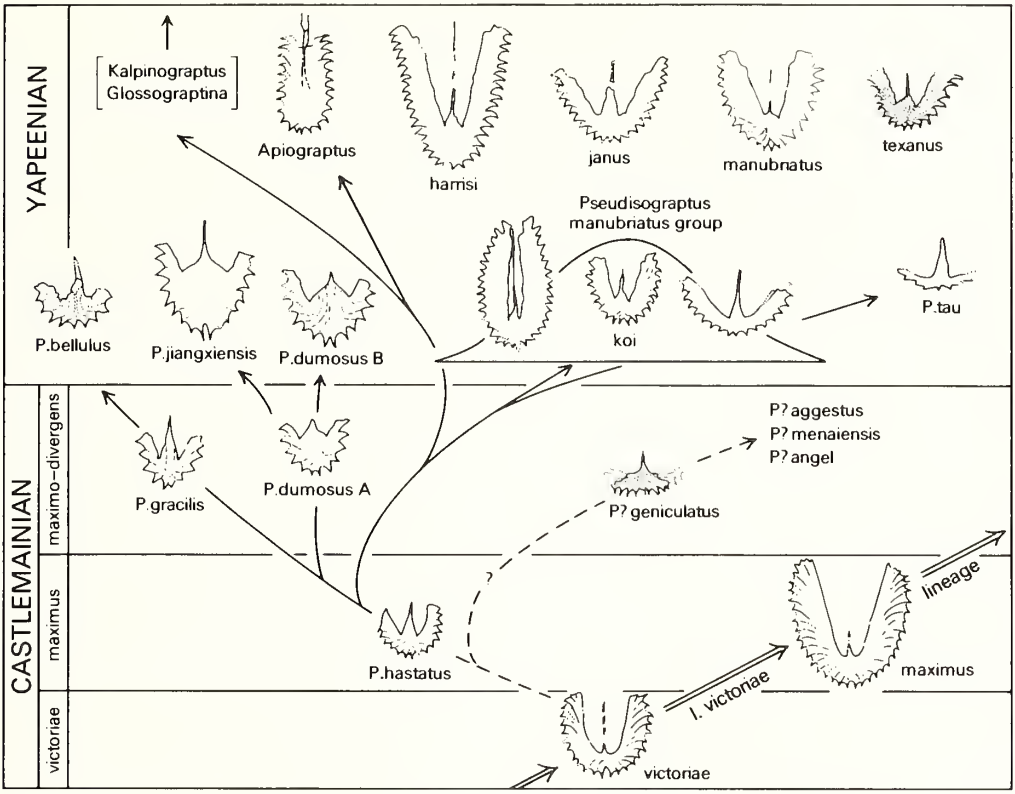
and the Glossograptina or it is apomorphic for the group and has been secondarily lost in *Kalpinograptus*. A second group includes *P. tau* and the *P. manubriatus* complex; it retains the (primitive) platycalycal structure and exhibits prothecal folds.

The second category also includes two species groups: in the first (*P. dumosus s.l.* and *P. jiangxiensis*) the manubrium is relatively expanded and stipes diminished in size; in the second (*P. bellulus* and *P. gracilis*) the primitive states for these features are retained.

Phylogeny. From the cladogram and stratigraphic ranges a tentative scheme of phylogenetic relationships can be derived (text-fig. 5). The earliest known manubriate isograptid, *P. hastatus* is also that which deviates least in morphology from isograptids of the *I. victoriae* lineage, previously suggested to be ancestral to the manubriate group (Cooper 1973). An ancestor at about the level of *victoriae* or *maximus* could have given rise to an early manubriate form by elongation of the sicula and proximal thecae and delay in the point of upward flexure of the stipes, thus producing a simple manubrium in an otherwise isograptid rhabdosome. A slight modification of distal thecae by 'thecal neoteny' would have given rise to a lower distal angle of inclination and a more inclined apertural margin. The result would have been a rhabdosome like that of *P. hastatus*. The strong outward deflection of proximal thecae, characteristic of manubriate species, was a later derived character. The *I. victoriae* lineage is thus tentatively taken as ancestral to the manubriate group.

The position of the *geniculatus* group of species is quite uncertain and the four species here included may not comprise a natural grouping at all. With their weakly developed manubrium they are shown to have diverged at an early stage but they bear little resemblance to early Australasian manubriate species and may have been independently derived.

All other manubriate forms are thought to have been derived from *P. hastatus* or a closely related coeval form. One major branch gave rise to the *P. manubriatus* complex and its derivatives, and to the *Apiograptus–Kalpinograptus* glossograptid group. The other branch produced *P. gracilis* and *P. bellulus* in one fork and the *dumosus–jiangxiensis* group in the other fork.



TEXT-FIG. 5. Phylogeny of the manubriate complex.

The most rapid diversification took place in the early Yapeenian, a time of extreme plasticity in the *P. manubriatus* complex. However, except for the glossograptines (which appear in the Darriwilian with *Glossograptus*, *Cryptograptus*, and *Paraglossograptus*) and the Llandeilo form *Kalpinograptus*, the manubriate stock had disappeared by the early Darriwilian.

Classification

There has been much recent discussion on principles and methods of biological classification and three main approaches to the practice have emerged, two of which are based on evolutionary relationships. The first, the cladistic method, adheres strictly to phylogeny (genealogy) whereas the second, the evolutionary method, incorporates both phylogeny and an estimate of anagenetic distance between taxa. Of particular interest to us here is the treatment of paraphyletic taxa (i.e. a group that includes a common ancestor and some, but not all, of its descendants); evolutionary taxonomists accept such groups as valid taxa whereas cladists reject them. Throughout this discussion terms and concepts used are as defined by Wiley (1981).

As far as the classification of graptolites is concerned, various approaches of earlier workers were discussed by Cooper and Fortey (1982) and a plea was made to adopt a phylogenetically based scheme. Their attempt at classification of the dichograptoids represents a first step towards such a scheme. In this work we are dealing mainly with lower taxonomic levels but the same phylogenetic principles apply. However, we recognize the usefulness of distinguishing and naming one class of paraphyletic taxa—stem groups—at least as an interim measure. It is convenient, for example, to be able to refer to the *Anisograptidae*, a stem group for several distinct lineages currently grouped under Dichograptidae. In this account, *Pseudisograptus* is a stem group.

If our inferred phylogeny (text-fig. 5) is correct, there are several important implications for classification and taxonomy:

1. Status of Glossograptina. Jaanusson (1960) raised Lapworth's Family Glossograptidae to suborder rank, stressing the 'considerable morphological discontinuity' which separates it from the diplograptids. Bulman (1963, p. 408) accepted this ranking and commented that the structural differences of both the glossograptids and diplograptids 'from the specialised isograptids in sicula, budding, and thecae are in my estimation so great as to eliminate this group from possible ancestry (cf. Thomas 1960)'. We are not concerned here with the relationships of the diplograptids but would claim that from the evidence now available the morphological gap separating the glossograptids from *Pseudisograptus* is much less than was formerly thought. Further, the ancestor of the glossograptids is most likely to be a pseudisograptid. This means that the glossograptids, including *Kalpinogratus* (following Finney 1978), plus *Apiograptus* (included here) form a sister group to *Pseudisograptus*, and the entire *Pseudisograptus*-glossograptid complex is a sister group to the remaining Isograptidae. The high ranking of the glossograptids no longer seems necessary, nor is it desirable when the rank of its sister groups is considered; it is here suggested that it be downgraded to family group rank and include the following genera: *Glossograptus*, *Paraglossograptus*, ?*Cryptograptus*, *Lonchograptus*, *Nanograptus*, *Kalpinograptus*, and *Apiograptus*. The key character for the group is the presence of pseudopericalycal structure. *Cryptograptus* differs in several respects (Finney 1978, p. 491) but is tentatively included since it is now known to include forms with comparable proximal structure (e.g. *C. marcidus*).

2. *Pseudisograptus* is a paraphyletic taxon because it includes the common ancestor and some, but not all, of its descendants (glossograptids are excluded). This seems preferable to the alternative of establishing new genera for the *gracilis–dumosus*, *hastatus*, and *angel* groups which would be necessary to maintain monophyletic taxa. Furthermore, all the genera would need their own family group names to match the family group status of the glossograptids.

3. Going further back in ancestry, if we are correct in assuming that the *I. victoriae* lineage (at about the stage of *victoriae/maximus*) is ancestral to the manubriate complex then, if cladist principles are strictly applied, members of the lineage beyond this stage (*maximus*, *maximodivergens*, *divergens*) form a sister group to that which includes the glossograptids and must be of equally high rank; members below this stage (*lunatus*, *victoriae*) belong in a different group of equally high rank. The problem is in fact circumvented by the grouping of all members of the *I. victoriae* lineage by Cooper (1973) and Harris (1933) within a single species which cannot therefore be subdivided. But the status of the group represented by *I victoriae* and its descendants must have rank equal to, or higher than that of, the entire manubriate complex (including the glossograptids).

Conclusions

The glossograptids (including *Kalpinograptus* and *Apiograptus*) form a monophyletic group, here distinguished as subfamily Glossograptinae. Its sister group is the paraphyletic *Pseudisograptus*, sole occupant of the new subfamily Pseudisograptinae. The two subfamilies are grouped in the family Glossograptidae, a monophyletic sister group to the Isograptidae which contains the sole subfamily Isograptinae *sensu* Cooper and Fortey (1982) but excluding *Pseudisograptus*. This arrangement minimizes the number of paraphyletic taxa and retains the most useful groupings of species and genera. *Corynoides* and *Corynites* are grouped in Glossograptinae, following Finney (1978).

Family GLOSSOGRAPTIDAE Lapworth, 1873 (emend.)
  Subfamily GLOSSOGRAPTINAE Lapworth, 1873
    Genera *Glossograptus*, *Apiograptus*, *Kalpinograptus*, *Lonchograptus*, *Nanograptus*, *Paraglossograptus*, *Corynoides*, *Corynites*, ?*Cryptograptus*
  Subfamily PSEUDISOGRAPTINAE (subfam. nov.)
    Genus *Pseudisograptus*
Family ISOGRAPTIDAE Harris, 1933 (emend.)
  Subfamily ISOGRAPTINAE
    Genera *Isograptus*, *Skiagraptus*, *Cardiograptus*, ?*Paracardiograptus*, ?*Oncograptus*

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens. Abbreviations used are as follows: P, Museum of Victoria, Division of Natural History and Anthropology, Melbourne, Australia; PR, New Zealand Geological Survey, Lower Hutt, New Zealand; NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, China; VG, Department of Geology, Victoria University of Wellington, New Zealand.

Fossil locality numbers cited for New Zealand are those of the New Zealand Fossil Record File.

Family GLOSSOGRAPTIDAE Lapworth, 1873 (emend.)

Diagnosis (revised). Stipes reclined to scandent; initial downward growth of stipes involving at least the first two thecal pairs; in earlier forms pronounced downward growth results in formation of a manubrium, but in later scandent forms only the first two thecal pairs retain this downward growth. Distal thecae are of relatively low inclination and of manubriate (or glossograptid) thecal form, with a pronounced ventral process in later forms.

Discussion. As conceived here the Family is a broad one, but it embraces forms each of which is thought to be more closely related to others in the group than to members of another family. It is comprised of two subfamilies: Glossograptinae and Pseudisograptinae.

Subfamily GLOSSOGRAPTINAE Lapworth, 1873

Diagnosis. Stipes reclined to scandent, initially monoserial or monoserial throughout; proximal structure pseudopericalycal; thecae of advanced manubriate form.

Discussion. The subfamily basically represents the Glossograptina of Jaanusson (1960) expanded only to include *Apiograptus* and *Kalpinograptus*. If *Cryptograptus* is correctly included, then the diagnosis should be emended to include forms with artus-type development, true pericalycal structure, and thecae which lack an apertural process. The presence of 'normal' development in *C. marcidus* (Hall) (see Finney 1978) suggests that artus development (and true pericalycal structure) in *C. tricornis* (Carruthers) (see Bulman 1945) was secondarily derived. The position of *Bergstroemograptus* Finney and Chen, 1984 is unclear; it combines glossograptid features of proximal structure with a thecal morphology which, at least superficially, resembles that of isograptids. For the time being, it is left *incertae sedis*.

Subfamily PSEUDISOGRAPTINAE subfam. nov.

Diagnosis. Stipes reclined; manubrium present; thecae of simple to advanced manubriate form; development of isograptid type; proximal structure platycalycal; prothecal folds present in some species.

Discussion. The subfamily contains one genus, *Pseudisograptus*.

Genus *Pseudisograptus* Beavis, 1972

[= *Arienograptus* Yu and Fang, 1981; ? = *Xiushuigraptus* Yu and Fang, 1983]

Type species. Didymograptus caduceus var. *manubriatus* T. S. Hall, by original designation.

Diagnosis. As for subfamily.

Discussion. Beavis's (1972) diagnosis was based on *P. manubriatus texanus* which is now known to be a somewhat aberrant form. The above emended diagnosis therefore makes no special reference to curvature and overlap of proximal thecae, and includes forms with no evidence of prothecal folds. It agrees with the diagnosis of Jenkins (1982). The key feature of *Pseudisograptus* is the presence of a manubrium; this feature can be regarded as a synapomorphy of the genus. The low inclination of distal thecae also appears to be synapomorphic. Those manubriate species in which isograptid symmetry is weak or lacking (*P. tau* and *P. aggestus*) are here interpreted as having lost the feature, present in their ancestors.

Arienograptus Yu and Fang, based on *A. jiangxiensis* (described below) is here synonymized with *Pseudisograptus*. *Xiushuigraptus* Yu and Fang, with *X. songxiensis* as sole species, appears to represent a growth stage of a species such as *P. m. janus*; it is tentatively placed in synonymy with *Pseudisograptus*.

The genus, as employed here, contains all known manubriate isograptid species.

Species. Species and subspecies included in the genus are listed together with an indication of the main name changes introduced here: *P. m. manubriatus* (T. S. Hall, 1914), *P. m. koi* ssp. nov. (= *P. manubriatus* Forms B and D of Cooper and McLaurin 1974 and Cooper 1979), *P. m. harrisi* ssp. nov., *P. m. janus* ssp. nov. (= *P. manubriatus* Form C of Cooper and McLaurin 1974), *P. m. texanus* ssp. nov. (= *P. manubriatus*, *sensu* Bulman 1968), *P. bellulus* sp. nov., *P. dumosus* (Harris, 1933) (= *P. dumosus* Forms A and B of Cooper 1973), *P. gracilis* (Ruedemann, 1947) (= *P. hastatus* Form B of Cooper 1973), *P. jiangxiensis* (Yu and Fang, 1981) (= *P. dumosus* Form C of Cooper 1973), *P. tau* (Harris, 1933) (= *Maeandrograptus tau* of previous authors), *P.? aggestus* (Harris, 1933) (=*M. aggestus* of Harris 1933), *P.? geniculatus* (Skevington, 1963), *P.? angel* Jenkins, 1982, and *P.? menaiensis* Jenkins, 1982.

These species are discussed below in the sequence that reflects related groups, rather than in alphabetical order.

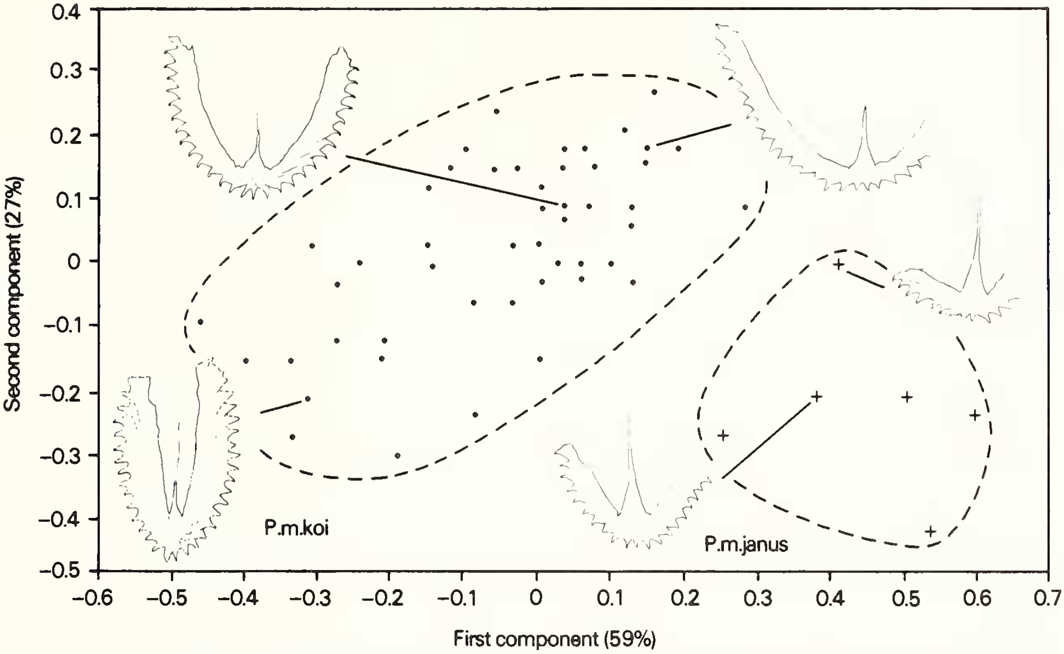
Pseudisograptus manubriatus (T. S. Hall, 1914) *s.l.*

Analysis of populations

New Zealand. The New Zealand population comes from a single locality in Jimmy Creek, Aorangi Mine, north-west Nelson, from strata thought to span a relatively short time interval. Its end members are so different that the average graptolite taxonomist would have no hesitation in separating them as distinct species. Compare, for example, text-fig. 12c and BB. The specimen of text-fig. 12c has curved stipes that are relatively narrow, of uniform width and (for isograptids) relatively low divergence angle, and a prominent manubrium; in the specimen of text-fig. 12BB the converse applies for each character. Furthermore, from the growth stages it is clear that the different rhabdosome forms result from different developmental 'pathways' and are not the result of late stage differences in development. On grounds of mature rhabdosome morphology and astogeny, therefore, it would seem that the two forms represent distinct species. Certainly, the differences between them are of the kind and order of magnitude of those generally taken as separating graptolite species. How, then, can they be included within a single subspecies?

The basic question to be answered is do the specimens all belong to a single population or can they be sorted into two or more populations? From inspection it is clear that the end members are linked by intermediates but what is the frequency distribution of specimens throughout the entire range of variation? To find out, we measured nine characters on each of the fifty-five *manubriatus*-like specimens from Jimmy Creek. Apart from a small group of six specimens, here separated out as *P. janus*, there is no clear evidence in the frequency distribution for any character of more than a single population, and most are strongly unimodal indicating a single population (text-fig. 14). The intermediate forms are more abundant than the end members for every measured character. In the PCA plot, based on five measured characters and accounting for 88 % of the total variation, the specimens plot as a compact group with no obvious within-group clustering, as might be expected if more than one population was present (text-fig. 6).

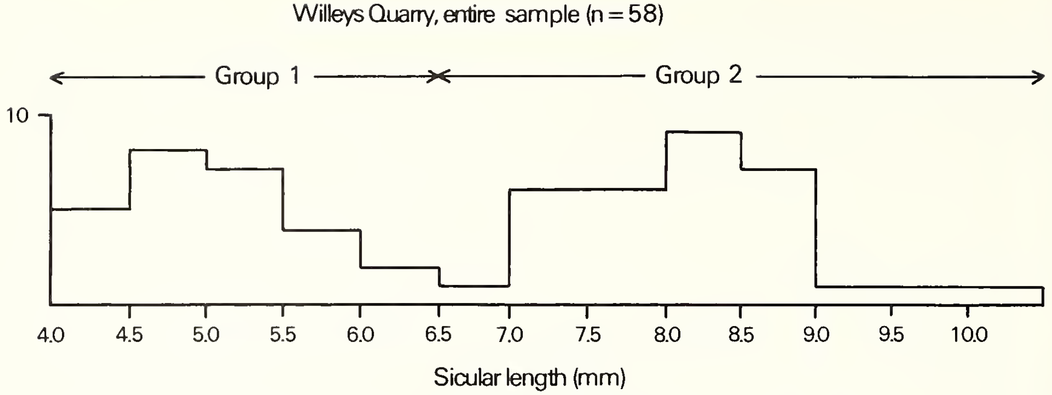
We conclude that, despite the wide range of rhabdosome forms present in the Jimmy Creek population, only a single taxon is represented. It has the greatest range of variability of any graptolite species with which we are familiar, reflected in the exceptionally high coefficients of variation for each measured character (7–30; see Appendix).



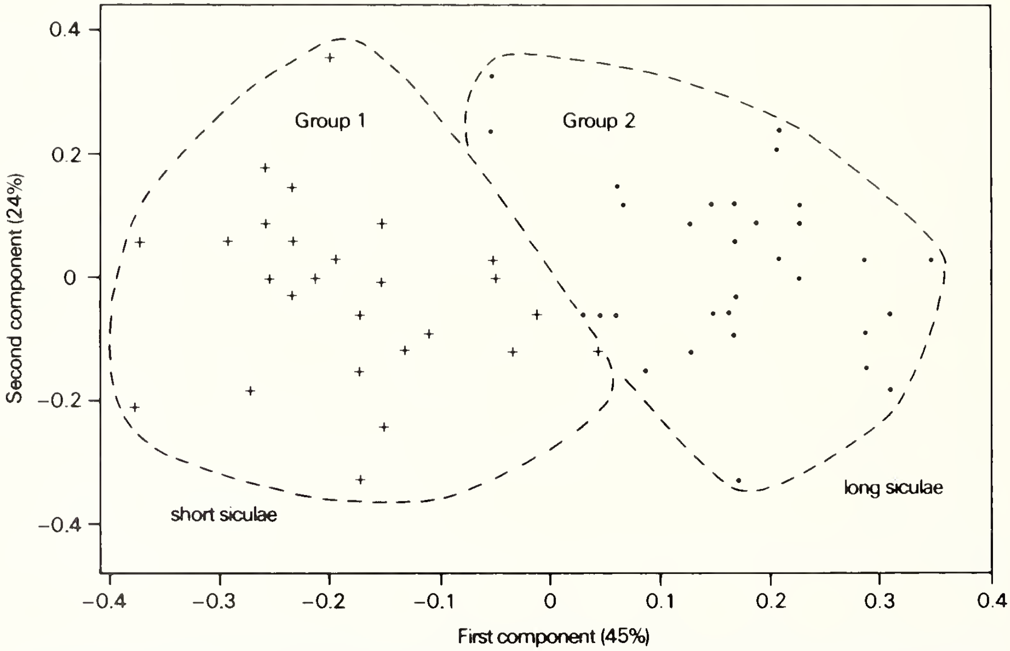
TEXT-FIG. 6. PCA plot of specimens from Jimmy Creek, north-west Nelson, New Zealand, showing two groups, *Pseudisograptus manubriatus janus* ssp. nov. and *P. m. koi* ssp. nov.

Australia. From inspection it was clear that the sixty measured specimens from Willey's Quarry, Macedon, Victoria, represented a range of morphological variation as great or greater than the material from Jimmy Creek. The measured characters were histogramed and it was immediately obvious that two groups could be distinguished on the basis of sicula length, those with siculae shorter than 6.5 mm (Group 1) and those with siculae longer than 6·5 mm (Group 2) (text-fig. 7); the same two groups are also suggested by manubrium length. No unequivocal groups emerged from a PCA plot, but when the Group 1 specimens with short siculae are distinguished on the plot they make up a distinct group with no overlap on the Group 2 specimens with long siculae (text-fig. 8). Thus the pattern of distribution derived from sicula length is consistent with that based on the two major PCA axes (derived from all measured characters), strongly suggesting that two populations are present.

Group 1, with short siculae, includes forms ranging from those that resemble Hall's (1914, pl. 17, fig. 12) figure of the type to forms matching those referred to *P. m. koi* in New Zealand. Could this group itself be comprised of more than one population? To test this possibility the same procedure was employed. Those forms with short broad manubria, as in the type form, are readily separated on a histogram of manubrium angle (Text-fig. 14D). On a PCA plot they form a loose



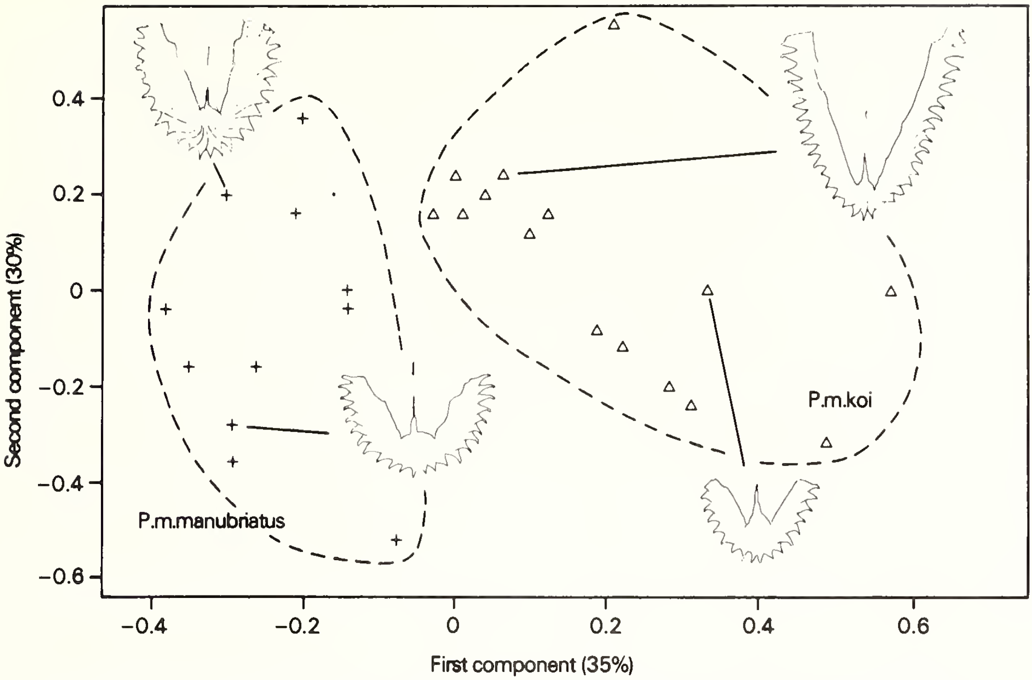
TEXT-FIG. 7. Frequency histogram of all specimens from Willey's Quarry, Victoria, showing two populations: Group 1 with short siculae and Group 2 with long siculae.



TEXT-FIG. 8. PCA plot of all specimens from Willey's Quarry, Victoria. Those with short siculae (Group 1) occupy a field with no overlap on that of specimens with long siculae (Group 2).

but largely distinct group (text-fig. 9). A few specimens (e.g. text-fig. 13C) are transitional in morphology and could be referred to either group, suggesting an overlap between groups. Group 1 is therefore taken as comprising two adjacent or overlapping populations, here referred to *P. m. manubriatus* and *P. m. koi* ssp. nov.

Group 2, with long siculae, appears to represent a single taxon, here recognized as *P. m. harrisi* ssp. nov. with the exception of two specimens (text-fig. 13H, I) which match well with New Zealand specimens of *P. m. janus*. On the PCA plot of Group 2 forms, the two specimens lie in one corner (text-fig. 20).



TEXT-FIG. 9. PCA plot of Group 1 specimens (short siculae) from Willey's Quarry, Victoria.

Thus the Willey's Quarry specimens are referred to four different pseudisograptid taxa.

The four Australasian populations recognized (*P. m. manubriatus*, *P. m. koi*, *P. m. harrisi*, and *P. m. janus*) are centres of clustering within a continuum representing the full morphological range of the species, *sensu lato*. No clear morphological gaps separate any one population from all others; each population is linked to at least one of its sister populations by specimens transitional in morphology between the two. For this reason they are best regarded as subspecies rather than as distinct species, and are interpreted as populations that had not become genetically isolated.

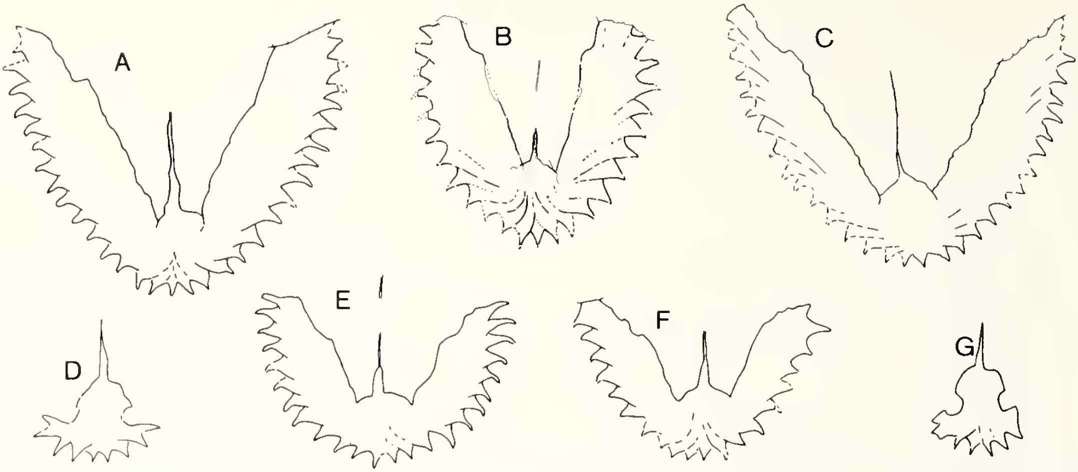
Pseudisograptus manubriatus manubriatus (T. S. Hall, 1914)

Plate 24, figs. 7 and 8; text-fig. 10

1914 *Didymograptus caduceus* var. *manubriatus* T. S. Hall, pp. 108–109, pl. 17, fig. 12 (*non* fig. 13 = *Pseudisograptus hastatus*).
1933 *Isograptus manubriatus* (T. S. Hall); Harris, pp. 102–104, pl. 6, fig. 1*f* and *h*; text-figs. 41–43.
1968 *Isograptus manubriatus* (T. S. Hall); Skevington, fig. 2.
1974 *Pseudisograptus manubriatus* (T. S. Hall) Form A, Cooper and McLaurin, p. 78, fig. 1*a–d*.

Identity of Pseudisograptus manubriatus. Hall (1914) established his new variety, *Didymograptus caduceus* var. *manubriatus* var. nov. with the following statement: 'Differs from the typical form by the immense size of the sicula, which at the point of separation of the branches is as wide as the branch itself. Thecae 10 in 1 cm. Branches diverging at 130° to 140°, and varying from 2 to 3 mm. in width. There is considerable range in the width of the branches, and the angle of divergence, but the great size of the sicula is remarkable. The variety is common at the recorded localities.' Two specimens were figured (pl. 17); that of fig. 12 is from a 'quarry in hard blue slate, one mile west of school on road from Woodend to Macedon' and labelled 'Type'; that of fig. 13 is from 'similar rock Steiglitz District', and labelled 'Cotype'.

The specimen from Steiglitz was referred by Harris (1933, p. 23) to his new species *Isograptus hastatus*, effectively establishing the specimen from Macedon as lectotype. Harris discussed the type locality and



TEXT-FIG. 10. *Pseudisograptus manubriatus manubriatus* (T. S. Hall), from Willey's Quarry, Victoria. A, mature rhabdosome, P 98216b; B, proposed neotype, P 103870; C, mature rhabdosome, P 42706.9; D, growth stage, P 42706.8; E, P 103878; F, P 103877; G, growth stage, P 103874. All ×3.

concluded that it was most probably a disused quarry known as Willey's Quarry, 'less than 1 mile west of the main Gisborne to Macedon Road, on the southern slope of the divide, about 38½ miles from Melbourne'. This conclusion is accepted here.

Harris makes no reference to having examined Hall's 'Type' specimen, the whereabouts of which is now unknown (Cooper 1973; Beavis and Beavis 1974). Efforts to locate the specimen by Museum staff have been unsuccessful and it is now considered lost. Harris figured eight specimens, representing growth stages, from Willey's Quarry, and a mature specimen from an 'isolated slab about 1 mile west of the old school site on the Main Divide, 3 miles south of Woodend', in his plate 6. A further four specimens from Willey's Quarry (his text-figs. 41-44) include two growth stages and two mature specimens.

Both Hall and Harris commented on the wide range of variation in rhabdosome morphology in the species, but Hall's material, of course, included forms now ascribed to *P. hastatus*. Harris commented (p. 111) that 'the range of variation is too great to be illustrated' but referred in his caption (p. 114) to varieties with long and short 'sicular regions'. Both varieties were said to be 'equally common'. Stipe divergence angle was also said to be variable.

A wide range of morphological variation is present among forms ascribed to the species. In New Zealand three informal forms were recognized by Cooper (1979) and Cooper and McLaurin (1974), all of which were thought to be distinct from the 'type form'.

In the present work, four subspecies are recognized among material from Willey's Quarry and a fifth in Texas. The identity of the nominate subspecies, *P. m. manubriatus*, is in some doubt because Hall's figure (1914, pl. 17, fig. 12) does not show sufficient morphological detail; it also appears to represent a specimen lying within one subspecies but near the morphological boundary with a neighbouring subspecies. This doubt can only be removed by designation of a neotype, and this course is proposed here.

EXPLANATION OF PLATE 24

Figs. 1-6, 9-12. *Pseudisograptus manubriatus koi* ssp. nov. from the Yapeenian of Jimmy Creek, Aorangi Mine, north-west Nelson, New Zealand. 1, PR 527, ×4. 2, growth stage, PR 411, ×6·5. 3, PR 508, ×4. 4, PR 354, ×4. 5, growth stage, PR 561, ×4. 6, PR 348, ×4. 9, PR 350, ×4. 10, PR 355, ×4. 11, PR 375, ×4. 12, PR 530, ×4. The specimens of figs. 12 and 13 correspond to Form D of Cooper (1979), all others correspond to Form B.

Figs. 7, 8. *P. m. manubriatus* (T. S. Hall) from the Yapeenian of Willey's Quarry, Macedon, Victoria. 7, neotype, P 103870, ×4. 8, topotype, P 42706.9, ×3·75.

PLATE 24


1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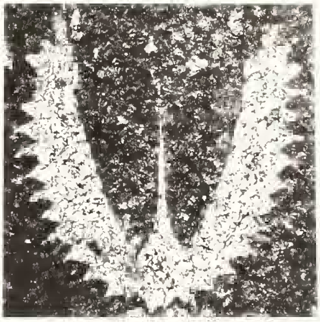
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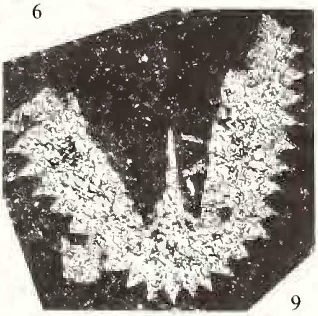
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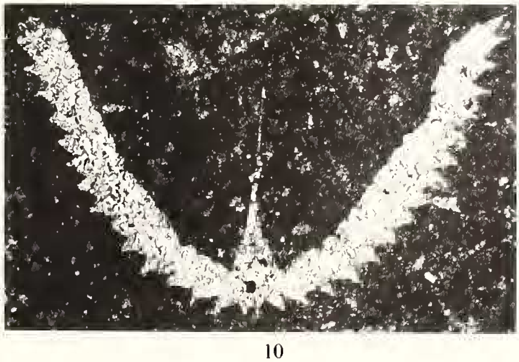
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11


12

COOPER and NI, *Pseudisograptus*

Neotype. Specimen P 103870 from Willey's Quarry, Macedon, Victoria, is here proposed as neotype (text-fig. 10B). A detailed comparison with Hall's figure is not possible because the figure lacks morphological detail; for example, the free proximal portions of the sicula and first theca do not show in Hall's figure and no details of rhabdosome structure are visible. However, in general outline the proposed neotype is a good match, except that the manubrium appears to be somewhat shorter and broader. Of the four subspecies recognized at Willey's Quarry, Hall's specimen most closely matches that of which the proposed neotype is clearly a member. It also accords with the prevailing concept of the 'type form' of *P. manubriatus* (Bulman 1968; Cooper and McLaurin 1974, Form A) in so far as rhabdosome outline is concerned. Beavis (1972) differed, claiming that the Texan specimen 'differs in several respects from the Victorian material, notably in the greater length and narrowness, relatively of the thecae; the two forms may be provincial variants or the differences may reflect the degree of compression, since the Texan specimens are in high relief'. However, from the topotypes figured here it can be seen that the differences specified are minimal, although it is conceded that on other grounds (proximal rhabdosome structure) the Texan material can be accorded separate subspecific status.

The proposed neotype is the only topotype specimen known to us in which the proximal region is preserved in sufficient relief to clearly define the growth paths (at least distally) of proximal thecae, a feature crucial to its distinction from the Texan subspecies. The neotype is preserved in obverse view.

Measured material. Fifteen specimens: P 98216a (transient to *P. m. koi*), 98216b, 98223c, 98226a–d, 42706, 103870, 103877, 103878, and four other specimens, together with several incomplete or poorly preserved specimens, from Willey's Quarry, Macedon, Victoria.

Horizon. Yapeenian; Willey's Quarry, Chinamen's Creek, and several other localities in Victoria.

Description. The rhabdosome is relatively small and compact; the manubrium is short and broad. The base of the manubrium makes a sharp angle with the dorsal stipe margin and in some specimens, such as the neotype (text-fig. 10B), it is clear that the dorsal stipe margin overlaps laterally on to the manubrium, growing around in a loop in the manner described by Cooper and McLaurin (1974, p. 80) in *P. manubriatus*, and here in *P. m. janus*.

The sicula averages 4·8 mm (range 4·3–5·9 mm) in length, its free proximal portion averaging 1·2 mm (range 0·8–2·0 mm; $V = 28$). Forms with long siculae tend to be those with long free proximal portions (see Appendix). Manubrium length is also variable (0·5–0·9 mm; $V = 27$), averaging 0·7 mm; manubrium width averages 1·9 mm (range 1·7–2·4 mm). The angle subtended by the manubrium shoulders ranges from 90° to 130°. Some details of proximal structure are seen in the neotype which is preserved in partial relief. The two thecal series are arranged symmetrically on either side of the rhabdosome midline and do not overlap each other as in the specimen from Texas described by Bulman (1968). Proximal thecae are long and recurved near their distal ends. The manubrium is comprised of the proximal portions of at least the first five pairs of thecae.

Stipes diverge from 310° to 335° and have generally straight dorsal margins which, in some specimens, show undulations suggesting the presence of prothecal folds. They reach 13 mm in length, are 2.6 mm (range 2·2–3·2 mm) wide proximally, and 3·1 mm (range 2·5–3·8 mm) wide distally. Stipe width is significantly negatively correlated with manubrium length and positively correlated with stipe divergence angle; forms with broad stipes tend to have more highly diverging stipes and shorter manubria.

Variation in stipe width does not interfere with the smoothly rounded ventral rhabdosome profile. Increase in stipe width is accommodated by a displacement of the dorsal stipe margin towards the rhabdosome midline (and encroachment on to the manubrium). In a few specimens there are considerable irregularities in the line of the dorsal stipe margin but these are not reflected in the ventral stipe margin; the apertural margins of thecae are aligned along a smooth curving line.

Thecae are spaced about five in 5 mm. They have a highly inclined apertural margin extended into a ventral process (advanced manubriate form).

Discussion. The subspecies forms a small group within the Willey's Quarry material. Modal forms are readily distinguished from the other subspecies, particularly *P. m. harrisi* and *P. m. janus*, by their short squat manubria (text-fig. 14D). In Willey's Quarry there are a few specimens that have a relatively long sicula and/or a deep infradorsal region; they are transitional in morphology towards *P. m. koi* or *P. m. harrisi*.

In gross rhabdosome morphology *P. m. texanus* closely matches the nominate subspecies; the distinction lies in their proximal structure. As seen in the neotype the two thecal series are symmetrically arranged on either side of the rhabdosome midline and are not superposed as in *P. m. texanus*.

Pseudisograptus manubriatus harrisi ssp. nov.

Plate 25, figs. 9 and 13; text-fig. 11

1933 *Isograptus manubriatus* (T. S. Hall) (*pars*); Harris, pp. 102–104, ?pl. 6, fig. 1*b*, *g*, *i*; text-fig. 44 (*non* pl. 6, fig. 1*f*, *h*; text-figs. 41–43 = *P. manubriatus manubriatus*; *non* pl. 6, fig. 1*a*, *c*, *d*, *e*, ? = *P. m. koi*).

Holotype. P 98222 from Willey's Quarry, Macedon, Victoria.

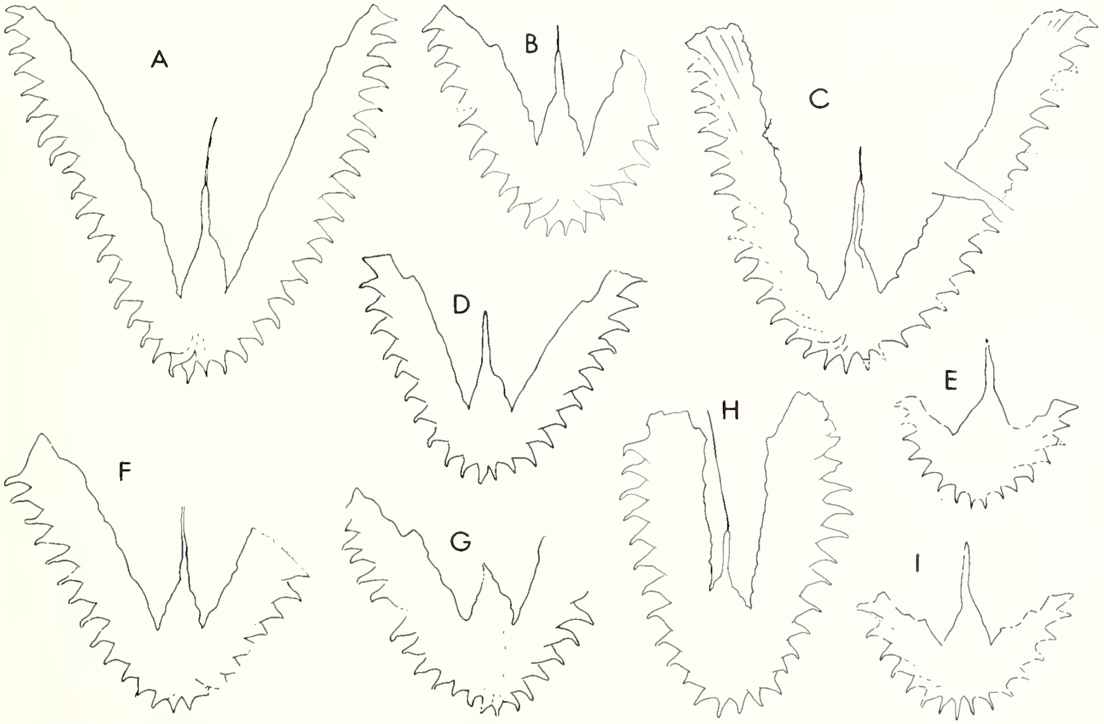
Measured material. Thirty-four specimens: P 42706, 98212, 98214, 98215, 98218, 98220a, 98220b, 98221, 98222, 98224, 98225a, 98229, 98217, 103880, 103881 and nineteen other specimens, from Willey's Quarry, Macedon, Victoria.

Horizon. Yapeenian.

Name. After W. M. Harris of Victoria, the first worker to elucidate relationships among the Victorian isograptids.

Description. The rhabdosome is relatively large and is variable in shape, ranging from an open V-shape to forms with nearly parallel stipes. The manubrium is generally large and wedge-shaped; its top is defined by a destinct break in slope from the free proximal portion of the sicula and th1^1. In forms with nearly parallel stipes the proximal portions of the stipes encroach upon the manubrium, reducing its apparent overall size (text-fig. 11H) The apex of the sicula is generally clearly marked, the nema being a thin thread in most specimens; in a few it is stout and passes gradually rather than abruptly into the sicula apex.

The sicula averages 8·1 (range 6·8–10·0 mm) in length, its free proximal portion averaging 2·1 mm but



TEXT-FIG. 11. *Pseudisograptus manubriatus harrisi* ssp. nov., from Willey's Quarry, Victoria. A, holotype, P 98222; B, P 103880; C, specimen transitional towards *P. m. janus* and with pronounced prothecal folding, P 98225a; D, specimen transitional towards *P. m. janus*, P 103886; E, immature stage, P 98220a; F, P 103883e; G, P 103883d; H, P 98221; I, immature stage, P 98220. All ×3.

varying widely (1–4 mm; $V = 35$). Forms with long siculae tend to have long free proximal portions. The manubrium length also varies widely, averaging 2·1 mm (range 1–3 mm; $V = 24$); manubrium width is 1·9 mm (range 1·2–2·4 mm). The angle subtended by the manubrium is 37–46° in most specimens. Structure of the manubrium is unknown. Interthecal septa can be traced a short distance from the ventral margin in the proximal region of the rhabdosome and suggest that the structure resembles that in *P. m. manubriatus*, with no marked thecal curvature and overlap of thecal series as in *P. m. texanus*. The infradorsal region is long and gives a 'deep' aspect to the proximal region. Infradorsal sicula length averages 3·7 mm.

Stipes in most specimens diverge at 320–330° and are either straight or have a slight dorsally-convex curvature. Undulations of the dorsal stipe margin suggest that prothecal folds are irregularly developed. Stipes reach 19 mm long, are 2·9 mm (range 2·4–3·4 mm) wide proximally and 3·1 mm (range 2·6–4·5 mm) wide distally. Distal stipe width is significantly correlated with manubrium length: forms with high distal stipe width tend to have shorter manubria (see Appendix). In most specimens the intersection between the manubrium shoulder and dorsal stipe margin is sharp and acutely angled.

Thecae are spaced nine or ten in 10 mm. They are of advanced manubriate form with a highly inclined apertural margin extended into a ventral process.

Discussion. The chief distinguishing features of the subspecies are the heavy, highly diverging stipes and large rhabdosome, the extended infradorsal region, and particularly the long sicula. It varies considerably in most characters, particularly manubrium width ($V = 16$), length ($V = 24$), free proximal sicula length ($V = 35$), and distal stipe width ($V = 17$) resembling *P. m. koi* in this respect. At first glance the specimens sometimes appear to be tectonically stretched members of other forms, such as *P. m. koi*. However, many slabs are available with randomly oriented specimens in which tectonic stretching would be immediately apparent; the effects of such distortion at Willey's Quarry, with the exception of a few slabs (not used), are regarded as not significant.

From *P. m. koi*, the subspecies is distinguished by its much longer sicula and greater infradorsal length (text-fig. 14A, E). *P. m. janus* has a generally larger manubrium and shorter infradorsal length (text-fig. 14C, E). From *P. m. manubriatus* and *P. m. texanus* the subspecies is readily distinguished by its larger manubrium and longer sicula (text-fig. 14A, C). *P. m. harrisi* is the most common form at Willey's Quarry, and is clearly represented among Harris's material by his text-fig. 44. Specimens of his pl. 6. figs. 1*b*, *g*, *i* are tentatively included; the manubrium of the mature specimen (fig. 1*i*) is obscured and its identity is uncertain. The subspecies is unknown outside Victoria.

Pseudisograptus manubriatus koi ssp. nov.

Plate 24, figs. 1–6, 9–12; Plate 25, figs. 3 and 4; text-figs. 12 and 13A–G, J

1973 *Isograptus manubriatus* (T. S. Hall) (*pars*); Cooper, pp. 84-88, text-fig. 22*a*–*g*, *l*–*n*, *p* (*non* text-fig. 22*h*–*k* = *P. m. janus*; *non* text-fig. 22*o*, *q* = *P. m. manubriatus*).
1974 *Isograptus manubriatus* (T. S. Hall); Tsai, p. 94, pl. 9, figs. 11–15 (*non* figs. 7–10); text-fig. 29.
1979 *Pseudisograptus manubriatus* (T. S. Hall) Forms B and D, Cooper, pp. 78–79, pl. 15, figs. *a*–*c*, *f*, *g*; text-fig. 60*a*, *b*, *d* (*non* pl. 15, fig. *h*; text-fig. 60*c* = *P. m. janus*).

Holotype. PR 508, from Jimmy Creek, north-west Nelson, New Zealand (text-fig. 12G).

EXPLANATION OF PLATE 25

Figs. 1, 6. *Pseudisograptus jiangxiensis* (Yu and Fang). 1, developmental stage, PR 564, ×6·5. 6, immature rhabdosome, PR 410, ×6·5.

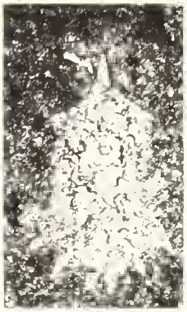
Figs. 2, 7. *P. dumosus* (Harris). 2, Form B, PR 414, ×5·3. 7, Form A, P 103885, ×6·5.

Figs. 3, 4. *P. manubriatus koi* ssp. nov. Growth stages, PR 567 and PR 563, ×6·5.

Figs. 5, 8, 10–12. *P. m. janus* ssp. nov. 5, PR 420, ×6·5. 8, PR 403, ×4. 10, PR 420, ×4. 11, PR 533, ×4. 12, immature rhabdosome, PR 562, ×4·4.

Figs. 9, 13. *P. m. harrisi* ssp. nov. 9, P 103881, ×3·3. 13, P 103883b, ×3·3.

Figs. 1–6, 8, 10–12, from the Yapeenian of Jimmy Creek, Aorangi Mine, north-west Nelson, New Zealand. Figs. 7, 9, 13, from the Yapeenian of Willey's Quarry, Macedon, Victoria.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COOPER and NI, *Pseudisograptus*

Measured material. Sixty specimens: PR 9–13, 311, 317, 319, 321, 324, 330, 348–350, 352, 355, 360, 363, 367, 375, 380–382, 385, 394, 395, 398, 399, 404, 405, 407, 408, 411, 416, 417, 419, 426–428, 430, 431, 434, 508–511, 515–524, 526–528, 530, from Jimmy Creek, north-west Nelson, New Zealand.

Horizon. Yapeenian in New Zealand and Victoria.

Name. Koi, a spike-shaped Maori digging tool, alluding to the spike-shape of the free proximal portion of the sicula and first theca.

Description. The sub-species displays extreme morphologic variation. The rhabdosome is relatively large and ranges from a wide open U-shape to forcipiform with parallel or even converging stipes. The manubrium is wedge-shaped and generally prominent, but in forms with parallel stipes it is partly obscured by the base of the stipes. The top of the manubrium is generally marked by a distinct break in slope from the free proximal portion of the sicula and $th1^1$. The apex of the sicula is sometimes difficult to distinguish from the base of the nema (see p. 315). The nema is stout and up to several centimetres long; a narrow strip of peridermal film adheres to the side in some specimens and in one the nema is forked (text-fig. 12M).

The sicula averages 5·4 mm (range 4·5–6·2 mm) in length, its free proximal portion averaging 1·5 mm (range 1·0–2·3 mm). The manubrium averages 1·6 mm (range 0·7–2·6 mm) in length and 1·5 mm (range 0·7–2·1 mm) in width. The angle between its shoulders is 40–50° in most specimens (text-fig. 14D). Manubrium width is significantly correlated (0·49) with manubrium length; where manubria are wide they tend also to be long (text-fig. 15A). Few details of proximal structure can be interpreted reliably from the flattened material, but proximal thecae of the two thecal series appear to be symmetrically arranged about the bilateral plane (as in *P. m. manubriatus* and *P. m. janus*) rather than overlapping (as in *P. m. texanus*).

Stipes range widely in divergence angle (280–360°) and curvature (from straight to strongly curved) (text-fig. 12). In forms with low stipe divergence angle (text-fig. 12A) the base of the manubrium generally passes smoothly into the dorsal stipe margin. In forms with high stipe divergence, the dorsal stipe margin commonly grows around in a loop, overlapping the base of the manubrium (Cooper and McLaurin 1974, p. 80). This has the effect of reducing the apparent width of the manubrium and increasing proximal stipe width; indeed stipe divergence angle has significant negative correlation with manubrium width (−0·664) and significant positive correlation with proximal stipe width (0·721) (text-fig. 15B).

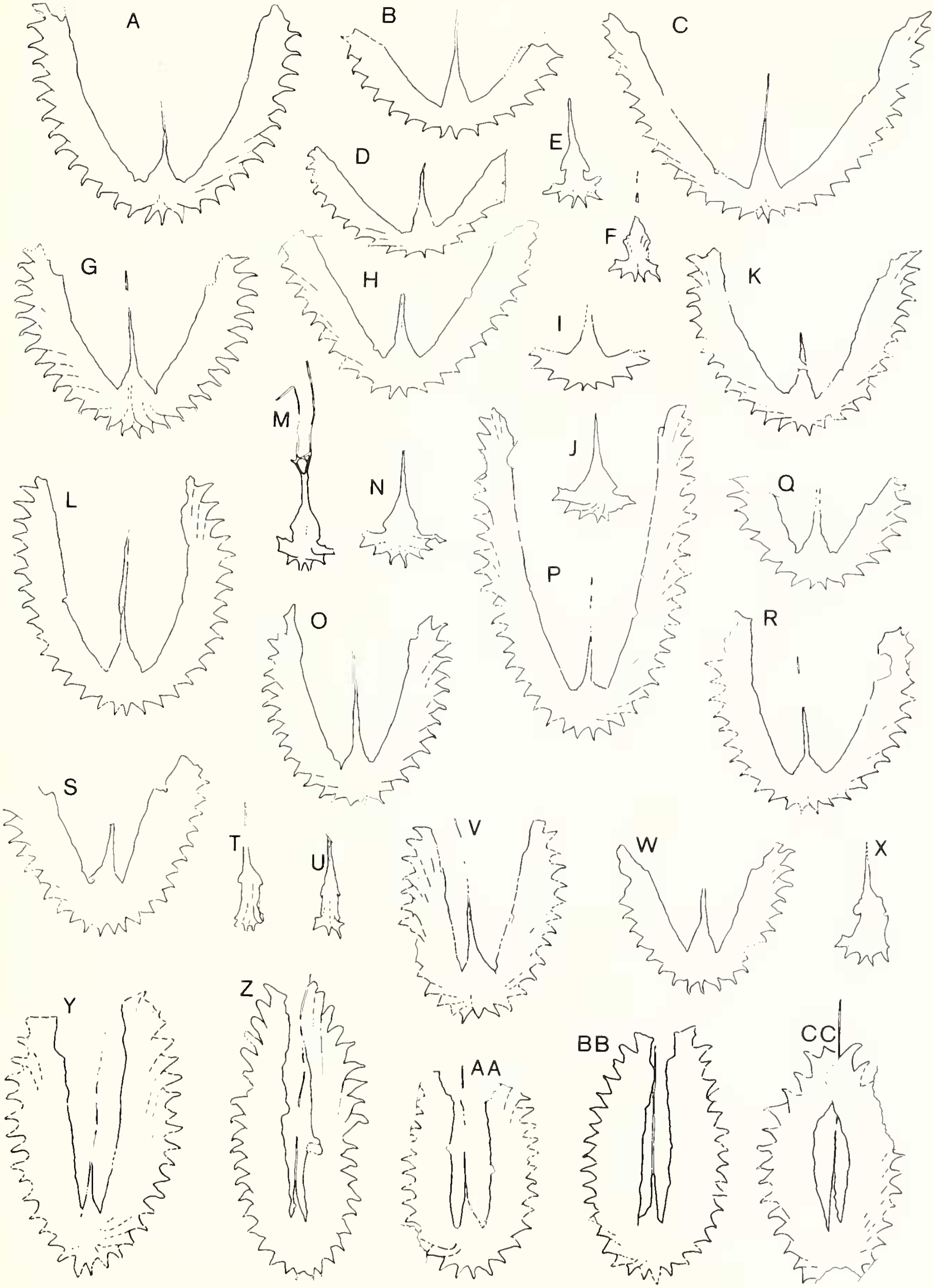
Stipes grow up to 15 mm long. In forms with straight stipes, stipe width is generally greatest at about mid stipe (where the 'distal' stipe measurement was made) and tapers slightly both proximally and distally; in forms with curved stipes, stipe width is approximately uniform. The result is that the ventral rhabdosome margin is always curved, whether or not the dorsal stipe margins are curved.

Thecae are extremely long; distal thecae are of low inclination (20–30°) and of advanced manubriate form. Apertural margins are highly inclined to the stipe axis and each bears a prominent ventral process. Thecal spacing is 5·0–6·5 in 5 mm.

Growth stages are distinctive, passing through a characteristic dumb-bell-shaped stage with the proximal portions of the sicula and $th1^1$ protruding prominently.

A few specimens, particularly those with wide open-shaped rhabdosomes, show a slight proximal a symmetry; the bilateral plane of symmetry is deflected towards one side (presumably the $stipe^1$ side) and there is a consequent weakening of the isograptid symmetry (e.g. text-fig. 12B, G). At its extreme, this tendency results in the complete loss of isograptid symmetry and acquisition of maeandrograptid symmetry. One specimen with maeandrograptid symmetry (text-fig. 12D) also differs from most other members of the population in the low inclination of its proximal thecae. In these features it approaches *P. tau* (Harris) and suggests an origin for that species. The specimen is linked with other members of the population via forms with proximal thecae of low inclination (text-fig. 12B).

TEXT-FIG. 12. *Pseudisograptus manubriatus koi* ssp. nov., from Jimmy Creek, north-west Nelson, New Zealand. A selection of rhabdosomes to show the range in rhabdosome form. A, PR 354; B, PR 319; C, PR 355; D, specimen with maeandrograptid symmetry, PR 554; E and F, growth stages, PR 567 and PR 563; G, holotype, PR 508; H, PR 417; I and J, immature specimens, PR 9 and PR 356; K, PR 515; L, PR 527; M and N, growth stages, PR 582 with branching nema and PR 418; O, PR 348; P, specimen with longest stipes observed, PR 524; Q, PR 550; R, PR 531; S, PR 350; T, PR 581; U, PR 578; V, PR 399; W, PR 370; X, growth stage, PR 560; Y, PR 13; Z, PR 367; AA, PR 428; BB, PR 375; CC, PR 556. Growth stages match mature forms as follows: I, J, and N represent a relatively open rhabdosome, such as K; E, F, and T represent the typical (modal) form, such as W; M represents a strongly reclined form, such as Y; U and X represent a form with parallel stipes, such as B. All ×3.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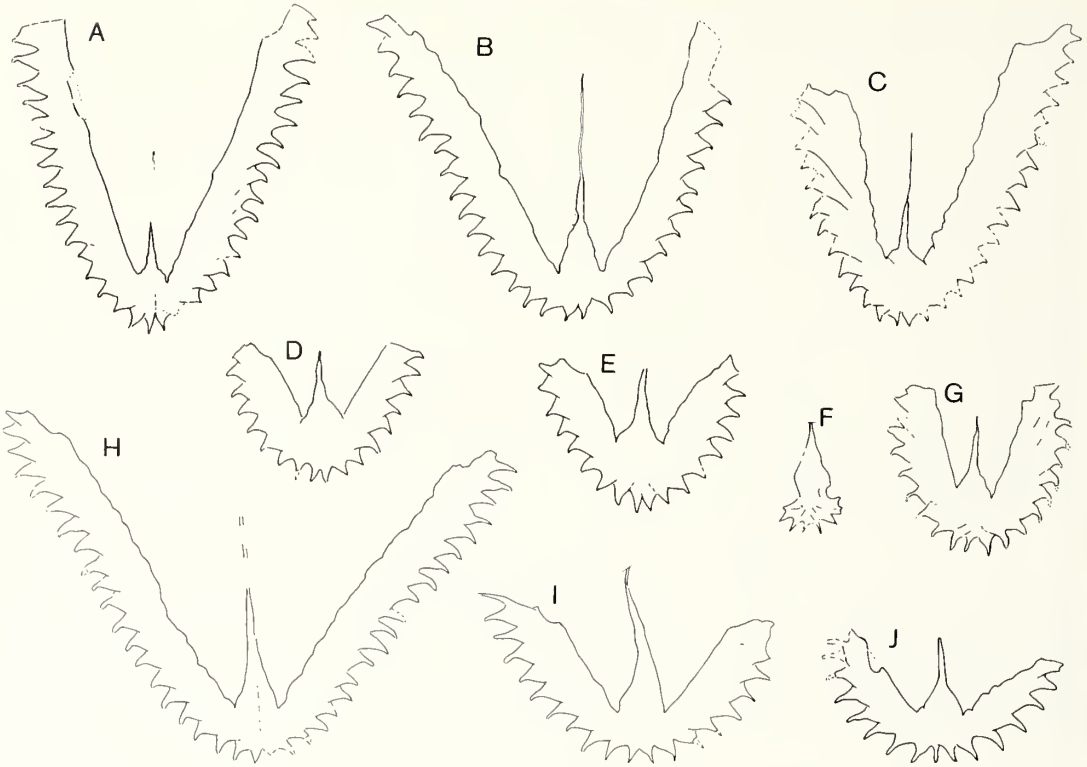

TEXT-FIG. 13. *Pseudisograptus manubriatus koi* ssp. nov. and *P. m. janus* ssp. nov., from Willey's Quarry, Victoria. A–G and J, *P. m. koi*: A, P 103879; B, specimen transitional towards *P. m. janus*, P 103882; C, specimen transitional towards *P. m. manubriatus*, P 98216a; D and E, immature specimens P 103874.1 and P 103876; F, growth stage, P 42706.4; G, P 103875; J, P 103873. H and I, *P. m. janus*: H, P 103872; I, P 103871. All ×3.

Fifteen specimens from Willey's Quarry, Victoria, lie within the range of the Jimmy Creek material in all measured characters, the mean value of each character agreeing well in the two localities. The Victoria specimens show a similarly wide morphological spread but the extreme members (i.e. Form D of Cooper 1979, and the wide open U-shaped forms) are not present (text-fig. 13A–G and J). However, a larger sample population from Willey's Quarry would be likely to include a wider morphologic range than that shown by the specimens to hand.

EXPLANATION OF PLATE 26

Figs. 1–7. *Pseudisograptus manubriatus janus* spp. nov., from the Ningkuo Formation, Fentoushan, Jiangshan, Zhejiang Province, China. 1, holotype, reverse view, NIGP 84733, ×12. 2, proximal part of manubrium showing origins of th1^2, th2^1, and th3^1, reverse view, NIGP 84736, ×50. 3, same, obverse/lateral view of manubrium (stipe^2 side) showing envelopment of earlier thecae by th3^2, ×25. 4, detail of base of manubrium of holotype on stipe^2 side, NIGP 84733, ×15. 5, proximal part of manubrium, obverse view, showing strongly impressed growth rings (normal to axis of growth) on the sicula and the envelopment of earlier thecae by th4^1, th3^2, and th4^2, NIGP 84736, ×25. 6, same, detail in lateral view of the origin, prothecal fold, and prothecal invagination of th3^1, ×70. 7, same, apical view showing 'crossing canal' formed by th1^2, and broken sicula and th1^1, ×30.

Fig. 8, *Pseudisograptus bellulus* sp. nov., from the same locality, but about 1 m higher in section. Rhabdosome complete except for apical portion of sicula and th1^1, lit from below to show thecal outlines, NIGP 84735, ×12.

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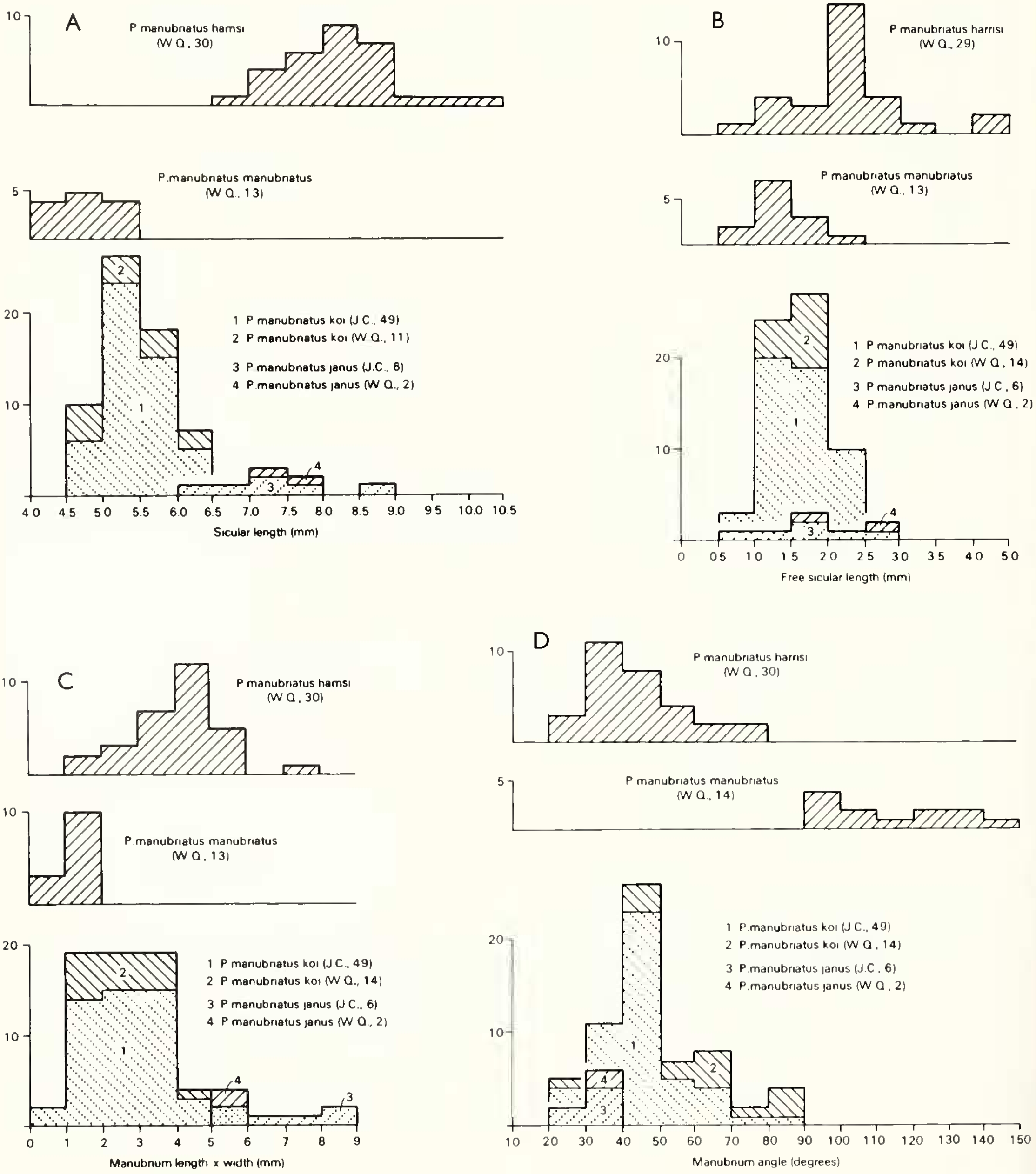
COOPER and NI, *Pseudisograptus*

Discussion. With its wide range of morphological variation (discussed above) it is not surprising that peripheral members of the subspecies approach sister subspecies in morphology. The distinction from *P. m. janus* is discussed with that form. In the Willey's Quarry material the subspecies is most easily distinguished from *P. m. manubriatus* by the proportions of its manubrium, reflected in the manubrium angle (text-fig. 14D). From *P. m. harrisi* it is distinguished by its shorter sicula length (text-fig. 14A) and 'shallower' proximal region, as reflected in its shorter infradorsal length (text-fig. 14E).

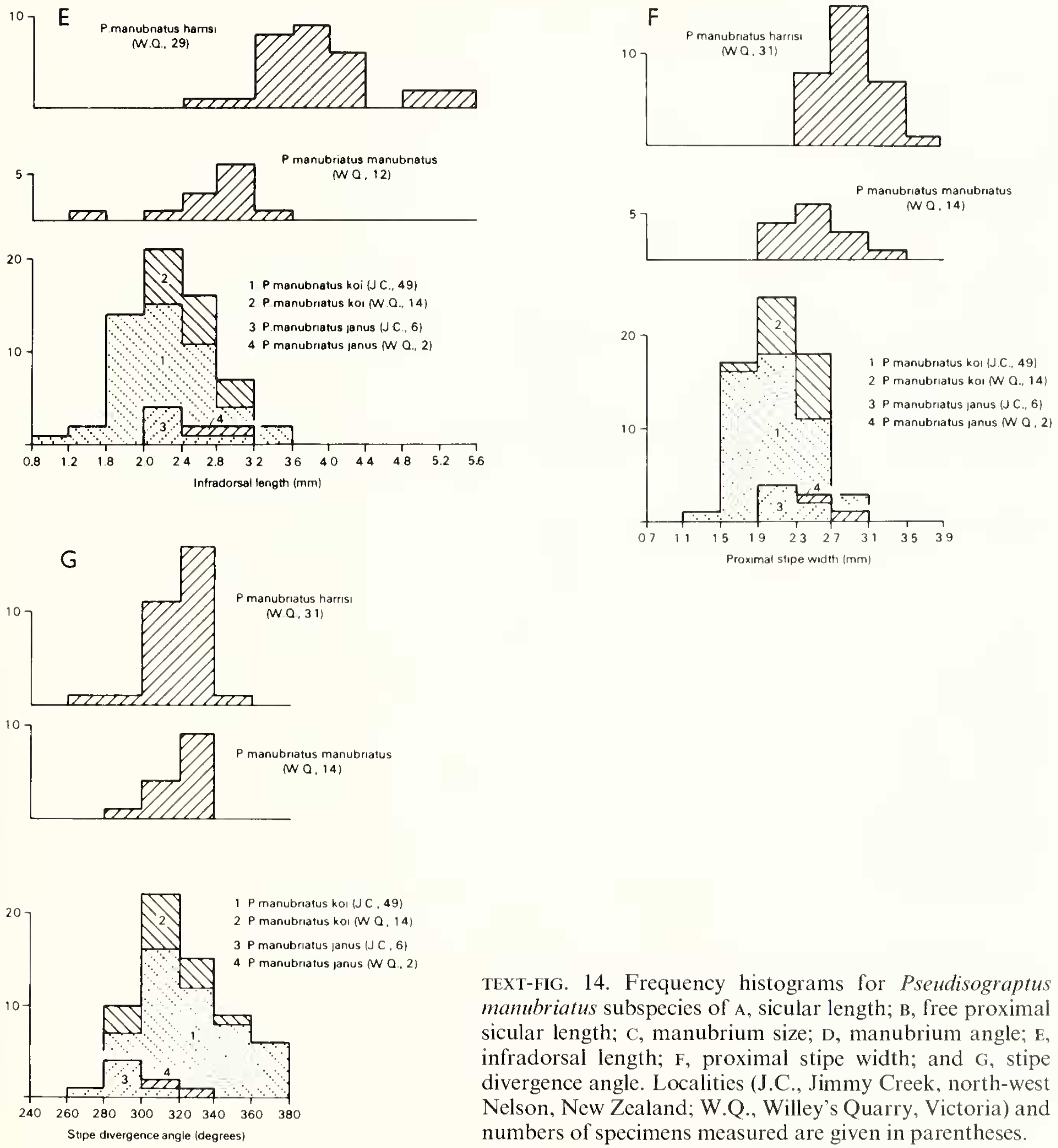


The range of forms figured by Tsai (1974, pl. 9, figs. 11–15, *non* figs. 7–10) from the *Isograptus gibberulus* (*I. victoriae*) Zone of Kazakhstan matches the Nelson forms well, and they are here included in the subspecies.

Pseudisograptus manubriatus janus ssp. nov.

Plate 25, figs. 5, 8, 10–12; Plate 26, figs. 1–7; Plate 27; text-figs. 13H, I, 16, 17

1973 *Isograptus manubriatus* (T. S. Hall) s.l. (*pars*); Cooper, pp. 84–88, text-fig. 22*h–k* (*non* text-fig. 22*a–g*, *l–q*).



TEXT-FIG. 14. Frequency histograms for *Pseudisograptus manubriatus* subspecies of A, sicular length; B, free proximal sicular length; C, manubrium size; D, manubrium angle; E, infradorsal length; F, proximal stipe width; and G, stipe divergence angle. Localities (J.C., Jimmy Creek, north-west Nelson, New Zealand; W.Q., Willey's Quarry, Victoria) and numbers of specimens measured are given in parentheses.

1974 *Pseudisograptus manubriatus* (T. S. Hall) *s.l.* Form C, Cooper and McLaurin, pp. 77–80, text-fig. 1*e–g* (*non* text-fig. 1*a–d*).

1979 *Pseudisograptus manubriatus* (T. S. Hall) *s.l.* Form C, Cooper and McLaurin; Cooper, pp. 78–79, pl. 15, fig. *h*; text-fig. 60*c*.

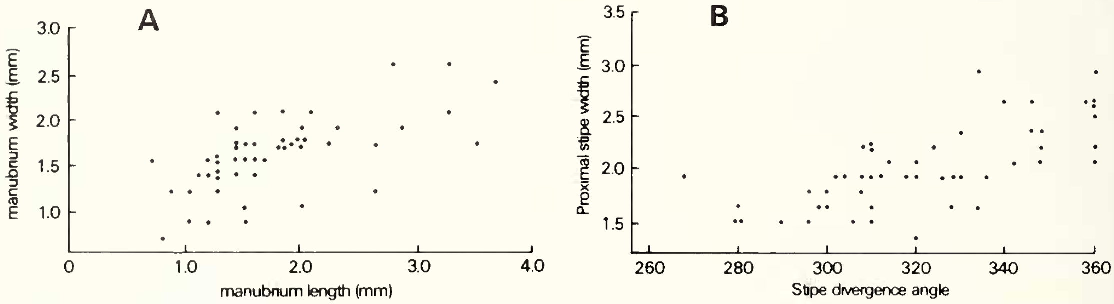
Holotype. Specimen NIGP 84733 (text-fig. 17F) from the Ningkuo Formation at Fentoushan, near Jiangshan, Zhejiang Province, China.

Material. Six measured specimens: PR 10, 340, 402, 403, 420, 533, and several immature specimens and growth stages, all flattened, from loc. S2/f540 of Cooper (1979, p. 97), Jimmy Creek, north-west Nelson, New Zealand; two specimens, P 103871, 103872, from Willey's Quarry, Macedon, Victoria, similarly flattened; eight specimens, NIGP 84731–84734, 84736–84739, from Fentoushan, near Jiangshan, Zhejiang Province, China, pyritized and preserved in full relief in shale. The Chinese material is preserved as an internal cast and reveals growth line details of the internal surface of the rhabdosome.

Horizon. The New Zealand and Victorian material is from the Yapeenian. The Chinese material is from horizons 9 and 11 in the section measured by Han Nairen *et al.* (1984) in the Ningkuo Formation, Fentoushan Section, near Jiangshan; it is associated with *Pseudotrigonograptus ensiformis* and (at horizon 11 only) *Cardiograptus amplus* and *Didymograptus hirundo*, equivalent to Yapeenian in age.

Name. Janus the Roman God with two faces, alluding to the different appearance of obverse and reverse aspects.

Description. The rhabdosome is large and V-shaped and resembles the V-shaped forms of *P. manubriatus s.l.* The sicula is very long, averaging 7·4 mm (range 6·2–8·6 mm) and the free proximal portion averages 1·6 mm (range 1·0–2·5 mm). The apex of the sicula passes into a stout nema which sometimes has a narrow adhering



TEXT-FIG. 15. *Pseudisograptus manubriatus koi* ssp. nov. from Jimmy Creek, north-west Nelson, New Zealand. A, manubrium width plotted against manubrium height, showing weak (but significant) positive correlation ($r = 0{\cdot}490$); B, proximal stipe width plotted against stipe divergence angle for fifty specimens, showing moderate positive correlation ($r = 0{\cdot}721$).

EXPLANATION OF PLATE 27

Figs. 1–9. *Pseudisograptus manubriatus janus* ssp. nov., from the Ningkuo Formation, Fengzu, Jiangshan, Zhejiang Province, China. 1, proximal part of manubrium, reverse view, NIGP 84734, ×25. 2, specimen in reverse view but in which the proximal portion has broken away to reveal impression of obverse side, NIGP 84731, ×13. 3, detail of the origin, prothecal invagination, and lateral 'flange' of th4^1, NIGP 84734, ×65. 4, lateral/reverse view of proximal part of manubrium showing origins of th2^2, th3^2, and th4^2, NIGP 84734, ×25. 5, complete specimen, the manubrium of which was removed and is shown in figs. 1, 3, 4, 7, and 8, reverse view, NIGP 84734, ×16. 6, growth stage, obverse view, NIGP 84732, ×12. 7, detail of origin of th3^1, lateral view, NIGP 84734, ×55. 8, same, lateral view of manubrium, ×25. 9, lateral/reverse view showing origin of th2^1 and the continuity of its growth (on right-hand side) around the prothecal invagination, NIGP 84736, ×120.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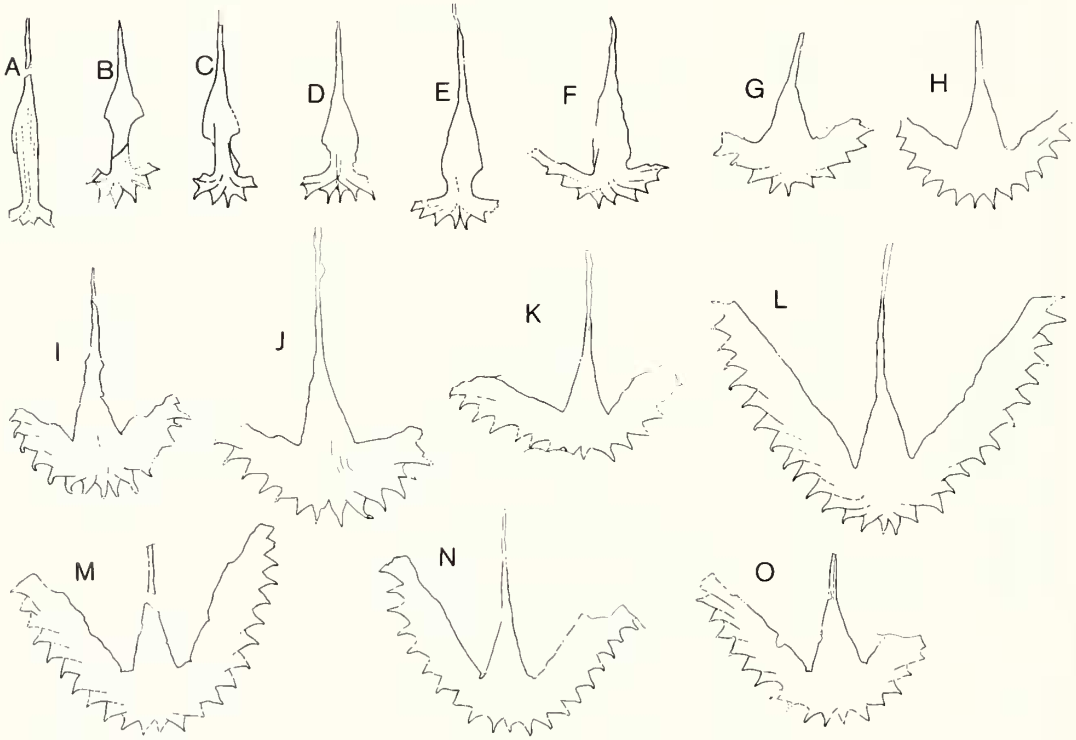
COOPER and NI, *Pseudisograptus*

strip of periderm as in *P. m. koi*. The manubrium is massive and shaped like a narrow wedge, averaging 2·2 mm (range 2·0–2·5 mm) wide and 3·3 mm (range 2·8–3·7 mm) long.

The stipes are sharply flexed and straight, reach 9·5 mm in length, and diverge at 290° (range 267–300°). In a few specimens (text-fig. 16N) the dorsal stipe margin appears to grow around in a loop and recross its earlier path, as in *P. m. koi*. They are widest in their mid regions where they average 2·3 mm (range 2·1–2·8 mm); proximally they average 2·2 mm (range 1·9–2·5 mm). The dorsal stipe margins of some specimens show undulations suggestive of prothecal folds, irregularly developed.

Form and inclination of distal thecae are like those of *P. m. koi*. Thecae are spaced about five in 5 mm.

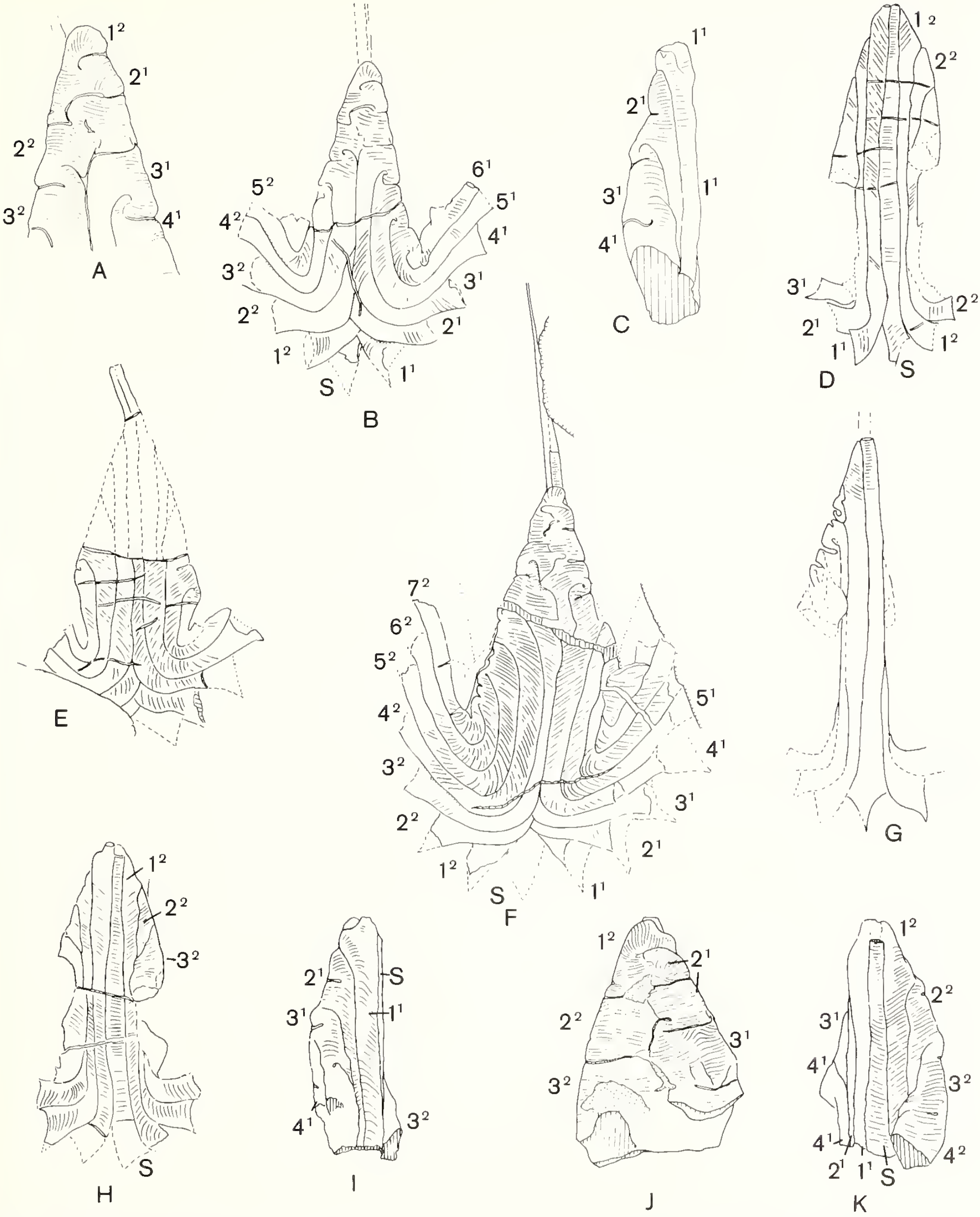
Growth stages are distinctive and readily distinguished from those of the coeval *P. m. koi* by their long sicula and gradually expanding manubrium.



TEXT-FIG. 16. *Pseudisograptus manubriatus janus* ssp. nov. B from Fentoushan, China; all others from Jimmy Creek, north-west Nelson, New Zealand. A–J, growth series: A, PR 434; B, Z8; C, PR 575; D, PR 558; E, PR 389; F, PR 542; G, PR 572; H, PR 538; I, PR 576; J, PR 562; K, specimen transitional towards *P. m. koi*, PR 402; L, largest specimen, PR 420; M, PR 533; N, PR 10; O, PR 340. All ×3.

Description of Chinese material—rhabdosome morphology. In the most advanced growth stage (text-fig. 17F) the manubrium is massive and stipes are barely developed. The specimen also shows the proximal, free portions of the sicula and $th1^1$. The sicula is at least 8 mm long, and 0·6 mm wide at the aperture. The sicula apex is not well defined as the sicula grades into the nema. The origin of $th1^1$ is also not clear but is high on the sicula, at least 1 mm above $th1^2$ and the top of the manubrium. Theca 1^1 grows down in contact with the sicula, the apertural regions of the two forming a symmetrical pair. $Th1^1$ is 7·5 mm long and of similar apertural width to the sicula.

The massive wedge-shaped manubrium varies in size and proportion among the four relatively mature unflattened specimens available. In the largest of these (text-fig. 17F, holotype) it measures 2·8 mm in length and about 2·1 mm in width, and incorporates the proximal portions of the first seven or eight pairs of thecae.



TEXT-FIG. 17. *Pseudisograptus manubriatus janus* ssp. nov., from Ningkuo Formation, Fentoushan, near Jiangshan, China. A–C, NIGP 84734: A, detail of manubrium clearly showing prothecal invaginations and initial upward growth of th1^2, ×15; B, complete specimen in reverse view, ×10; C, obverse/lateral view showing continuity of growth around prothecal invagination for th3^1 and th4^1, ×15. D, growth stage, NIGP 84732, ×10; E, reverse view, obverse impression revealed where proximal portion has broken away, NIGP 84731, ×10; F, holotype, reverse view, NIGP 84733, ×10; G, growth stage, NIGP 84739, ×10. H–K, NIGP 84736: H, growth stage similar to that of D, obverse view, showing envelopment of th1^2 and th2^2 by th3^2, ×10; I, obverse/lateral view (stipe^1 side) of proximal part of manubrium, ×15; J, reverse view of same, ×15; K, obverse/lateral view (stipe^2 side), ×15.

The manubria of other rhabdosomes are smaller and incorporate fewer thecae. Variation in the angle enclosed by the shoulders of the manubrium and in other proportions is best observed from the figures (text-fig. 17A–K). The obverse and reverse aspects of the manubrium differ to a remarkable degree. In obverse aspect the first three pairs of thecae grow down parallel to the sicula, flexing sharply outward near their distal ends. The fourth pair overlap the third pair and grow in towards the sicula (text-fig. 17K) before also swinging outwards to form part of the diverging reclined stipes. Growth lines on the sicula lie approximately normal to the growth axis whereas growth lines on all early thecae are strongly inclined to the growth axis, indicating that their apertures were directed away from the sicula throughout their development.

On the reverse side of the rhabdosome the growth paths of $th2^1$, $th2^2$, $th3^1$, $th3^2$, and (in holotype only) $th4^1$ completely overlap those of earlier thecae until near their distal ends, where they swing sharply away from the rhabdosome's midline and clearly reveal their plaited arrangement (text-fig. 17F). As a consequence, thecae are strongly flattened in cross-section and the manubrium has a triangular profile (text-fig. 19C). Rhabdosomal growth stages have the characteristic dumb-bell outline (text-fig. 17D, G) of manubriate isograptids, and closely resemble those of flattened specimens here referred to the species. As on the obverse side, growth lines are strongly inclined to the thecal growth axis.

The junction between the two thecal series (i.e. between $th3^2$ and $th3^1$ or $th4^1$) is straight and lies more or less in the rhabdosome's bilateral plane, as in *P. manubriatus s.l.*, but unlike *P. m. texanus* in which the line of junction is strongly displaced to the $stipe^1$ side (Bulman 1968, fig. 1).

Thecal apertures are not well preserved but, from outline impressions, had a pronounced ventral process.

The stipes are barely developed, even in the most mature specimen (text-fig. 17F); their initial angle of divergence can be estimated at about 310–320°.

Proximal structure and development. Development is of isograptid type and dextral mode. $Th1^2$ originates on $th1^1$, about 1 mm down and on its left-hand side (text-fig. 17A, B, F, J). It grows initially up and across $th1^1$ and the sicula before growing down on the right-hand ($stipe^2$) side of the rhabdosome. It is thus left-handed in origin and dextral in mode of development in the sense of Cooper and Fortey (1982, pp. 173–174), resembling *Dicranograptus* and the later diplograptids (Bulman 1970, pp. V78–81). It gives rise to $th2^1$ which grows across to the $stipe^1$ side and down. The downward growth is interrupted by a deep invagination in the dorsal wall, forming a 'recumbent' fold in the protheca (text-fig. 17C, I), following which the theca rapidly expands to extend well across the rhabdosome midline on the reverse side (text-fig. 17J).

$Th3^1$ arises on the right-hand side of $th2^1$ (i.e. on the reverse side of the rhabdosome) and immediately develops a prothecal fold with a deep invagination. It expands rapidly to envelope $th2^1$ completely on the reverse side, the fuselli reaching to the midline of the rhabdosome.

$Th4^1$ arises on the dorsal side of $th3^1$ (i.e. in the normal position) and immediately forms a similar prothecal fold to that of $th3^1$. It expands rapidly and soon completely envelops $th3^1$ on the *obverse* side, even encroaching on to $th2^1$ in one specimen (text-fig. 17I). This theca thus overlaps earlier thecae, but on the opposite side of the rhabdosome to that of its predecessors. On the reverse side of the rhabdosome it either grows down beside $th3^1$ (text-fig. 17B, E) or eventually overlaps it completely (text-fig. 17F).

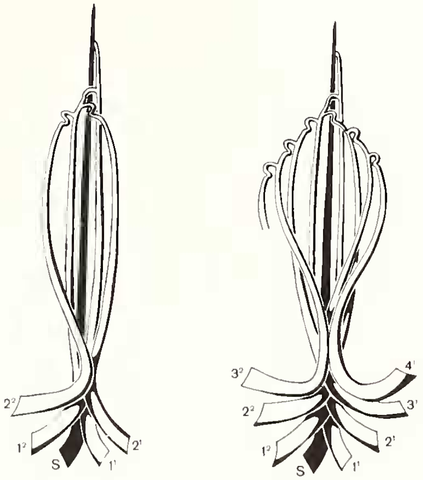
We have no detailed growthline data on the development of $th5^1$ and $th6^1$ but their prothecal folds appear to be less pronounced than those of preceding thecae. In text-fig. 17A, B, and E the downward growth of $th5^1$ is brief before it swings around to become part of the upward growing and diverging $stipe^1$. In text-fig. 17B, $th6^1$ commences its upward growth almost immediately after its origin. It is thus the last theca on the $stipe^1$ side to form part of the manubrium; subsequent thecae grow out along the stipe for their entire length. However, in text-fig. 17F the downward growth of early thecae prior to their outward deflection is more pronounced, and more thecae become incorporated in the manubrium. Thus $th6^1$ and probably $th7^1$ grow initially downwards, as part of the manubrium before bending sharply upwards.

In the axillary region, where the dorsal stipe margin joins the shoulder of the manubrium, there is a lateral overlap of thecae.

In the holotype (text-fig. 17F) the first upward growing theca on the $stipe^1$ side ($th8^1$) appears to originate on the right-hand side of its parent $th7^1$ (i.e. on the reverse side of the rhabdosome); it laps on to the prothecal portion of $th6^1$ in its upward growth. The dorsal stipe margin thus traces a loop, growing around and recrossing the line of its earlier path, a feature noted by Cooper and McLaurin (1974, p. 80).

On the $stipe^2$ side of the rhabdosome $th2^2$ arises on the dorsal side of $th1^2$, forms a small prothecal fold with a deep invagination, then rapidly expands to completely envelope $th1^2$ and reach across to the rhabdosome's midline (text-fig. 17A, J). $Th3^2$ similarly arises on the dorsal side of $th2^2$, forms a prothecal fold with deep invagination, and expands rapidly to completely envelope $th2^2$, after which it grows down in contact with $th3^1$ on the reverse side of the rhabdosome. The sicula, $th1^1$, $th1^2$, $th2^1$, and $th2^2$ are thus all completely enveloped on the reverse side of the rhabdosome by the pair th3^1 and th3^2. In the holotype th3^2 is eventually joined by th4^1 and this pair together overlap all earlier thecae.

Th4^2, like its opposite number th4^1, arises with a prothecal fold on the dorsal side of its parent theca and then expands rapidly on the *obverse* side of the rhabdosome to eventually completely overlap th3^2. On the reverse side it grows down in contact with th3^2.



TEXT-FIG. 18. Thecal diagram for *Pseudisograptus manubriatus janus* ssp. nov., based on specimens from the Ningkuo Formation, Fentoushan, near Jiangshan, China.

The origins of th5^2 and th6^2 are not well preserved in any specimens but, from the specimen of text-fig. 17F, they are assumed to be essentially like that of their opposite numbers, th5^1 and th6^1. In this same specimen, th7^2 is the last theca with a significantly downward growing component. Only a fragment of the proximal portion of th8^2 is preserved but it appears to arise on the obverse side of the rhabdosome (i.e. right-handedly) as does its counterpart, th8^1. In the specimen of text-fig. 17B, however, the first upward growing theca of each stipe originates left-handedly, indicating an opposite sense of torsion.

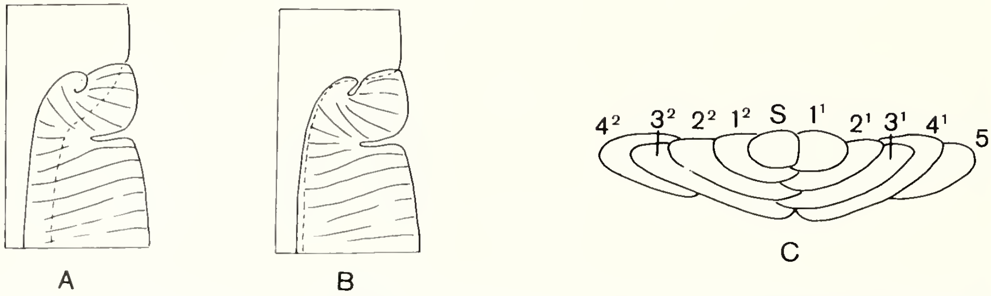
As a consequence of the tendency for proximal thecae to overlap earlier thecae and curve towards the rhabdosome midline half-way down the manubrium, growth stages take on a characteristic dumb-bell shape (text-fig. 17D, G; Cooper and McLaurin 1974, text-fig. 1*f*).

External morphology of prothecal folds. The prothecal folds described above differ from the 'normal' prothecal folds seen in sinograptids in that they produce only a slight protrusion or node in the dorsal rhabdosome margin. Instead of growing up and around in an inverted U-shape, the protheca curves around towards the rhabdosome's midline before doubling sharply back on itself to leave a deep invagination in its dorsal margin. At the same time it expands laterally, with later fuselli lapping on to earlier fuselli to form a flange analogous with the involute spire of nautiloids (text-fig. 19A). The structure shows well in the prothecae of th4^1 and th3^2 in text-fig. 17A and of th3^1 in text-fig. 17I. An alternative interpretation of this structure is possible and is shown in text-fig. 19B.

It is worth noting that the plate-like structure formed by the invagination in the dorsal prothecal wall is clearly visible in our specimens because they are *internal* moulds. This structure may not be very apparent where the periderm is preserved and morphology can be inferred only from the external surface.

Discussion. The flattened Nelson and Victorian specimens bear the distinctive massive manubrium and long sicula of the Ningkuo Formation specimens and share similar growth stages. No Chinese specimens have developed stipes but, from the incipient stipes present, stipe divergence angle was probably somewhat greater (325–330°) than in the Australasian specimens (267–300°). However, apart from this possible difference, specimens from the three regions match well and are here included in the same sub-species. The Nelson specimens represent the informal *Pseudisograptus manubriatus* Form C of Cooper and McLaurin (1974) and Cooper (1979).

The unflattened material from the Ningkuo Formation (*P. bellulus* and *P. m. janus*), together with the Texan specimen of *P. m. texanus* described by Bulman, provides the only detailed morphologic information on the proximal structure of manubriate species, and in particular, the structure of the manubrium. It is perhaps surprising that such an elaborate structure should show variation in such a fundamental feature as the number of thecae involved in its formation. The variation is, however, in keeping with the variation in size and proportions of the manubrium in flattened material of this and all other manubriate species.

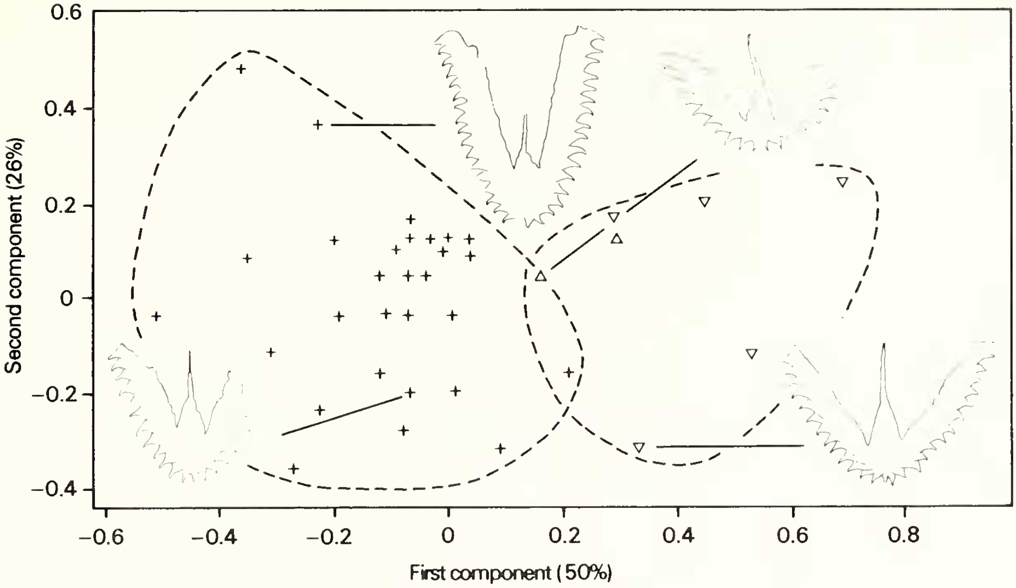


TEXT-FIG. 19. *Pseudisograptus manubriatus janus* ssp. nov. A and B, prothecal morphology based on th4^1 in specimen X33. A, the developing protheca envelops the preceding theca (th3^1, outlined by dashed line) and expands laterally near its origin such that later fuselli lap on to earlier fuselli to produce a flange; B, alternative interpretation in which the 'flange' represents a sharp re-entrant loop in the growth path of the developing protheca—this interpretation requires that there is minimal envelopment of the preceding theca and is, in our view, less likely. C, transverse section of rhabdosome at the level of th5^1, based on specimen of text-fig. 17F.

The number of thecae involved in the manubrium, and hence the point of flexure in the dorsal stipe margin that defines the manubrium base, is determined by the growth paths of the first few pairs of thecae. Those specimens in which the sicula and proximal thecae continue their downward growth to a greater than average length before deflecting outwards allow room for a greater than average number of thecae to assume initially downward growth and thus produce a longer and larger manubrium. An interesting implication of this control, or influence, on subsequent thecal growth pattern by earlier-formed thecae is that a feed-back mechanism probably exists to guide later thecal zooids in the growth direction of their thecae and, particularly, when to make the sharp flexure and assume upward growth. Feed-back is presumably provided by the thecal zooid 'feeling' ahead, and can be regarded as a special case of the feed-back mechanism that guides the growth paths of thecae at the distal end of the stipe. The sicula and initial thecae of *P. m. janus*, and indeed of all manubriate species, play an important role in influencing the size, shape, and subsequent development of the rhabdosome.

In New Zealand *P. m. janus* is most readily confused with *P. m. koi* which is found in the same beds. It is most easily distinguished by the size and characteristic wedge-shape of its manubrium. Manubrium size (length × width) is larger than the largest manubria in *P. m. koi*. There is relatively little variation in stipe divergence angle (unlike *P. m. koi*, which ranges widely) and the stipes are always straight (not commonly curved as in *koi*). Sicula length is generally greater than that of *P. m. koi*, and manubrium length + infradorsal length (a measure of the 'depth' of the proximal region) is also greater (text-fig. 14A, C, E, G).

On the PCA plot, *janus* plots as a group distinct from *koi* (text-fig. 6) but with a relatively wide scatter. One specimen (shown at the top of the group) is morphologically transitional towards the *koi* group, raising the question of whether or not it should be placed with the latter. On the reclassification test, however, no change was made to the original assignment, so it is here included with *janus*.



TEXT-FIG. 20. PCA plot of the specimens with long siculae (Group 2; *Pseudisograptus manubriatus harrisi* ssp. nov. and *P. m. janus* ssp. nov.) from Willey's Quarry, Victoria, together with the six specimens of *P. m. janus* from Jimmy Creek, north-west Nelson, New Zealand, showing slight overlap in their fields of morphology.

From *P. hastatus*, *P. m. janus* is distinguished by its much larger manubrium, longer sicula, and strong outward deflection of proximal thecae. From *P. m. manubriatus* the subspecies is readily distinguished by its longer sicula and manubrium size and proportions.

Pseudisograptus manubriatus texanus ssp. nov.

1968 *Isograptus manubriatus* (T. S. Hall); Bulman, pp. 212–214, figs. 1 and 2.

Diagnosis. *Pseudisograptus* with the size and outline of *P. m. manubriatus* but with the second thecal series overlapping the first in the proximal region, causing the line of junction between the two on the reverse side to be strongly displaced towards the stipe^1 side, as seen in reverse view.

Holotype. SM A60314, in the Sedgwick Museum, Cambridge, from the Port Pena Formation, Marathon, Texas, is here nominated as holotype.

Horizon. Berry (1960) gives the range of *P. manubriatus* in the Marathon section as Zones 8, *Isograptus*, and 9, *Paraglossograptus tentaculatus*.

Name. From Texas, the region from which the type, and only specimen, comes.

Discussion. From Bulman's illustration, the Texas form is indistinguishable from *P. m. manubriatus* in size and rhabdosome outline shape. The only significant point of difference lies in the incipient pseudopericalycal structure and symmetry of the manubrium; the second thecal series overlaps the first in the proximal region such that the line of junction between the two on the reverse side (i.e. between th2^2 and th3^1) is strongly displaced towards the stipe^1 side. Thus the origins of th4^1 and th5^1 which form part of the manubrium are obscured from view on the reverse side, and the reverse face of the manubrium is composed entirely of thecae of stipe^2, apart from th3^1.

Although at first glance the proximal structure looks very different from that of other manubriate species, such as *P. m. janus* and *P. m. manubriatus*, it can be simply derived from them by displacing the growth paths of proximal thecae about the rhabdosome midline axis in an anticlockwise rotational sense. Such a rotation would result in the early thecae of the first thecal series overlapping subsequent thecae at the base of the manubrium, as shown by Bulman's Fig. 2c. The structure could be brought about by a relatively minor alteration in the development programme of the rhabdosome. The final result, however, is distinctive and appears to be unique among pseudisograptid species. It may eventually warrant separation of the Texan material as a distinct species.

So far as is known the subspecies is confined to the Texan material, but its presence in Victoria is hinted at by a specimen from Chinaman's Creek in Victoria (Cooper and McLaurin 1974, text-fig. 1*d*) in which the thecal series may be superposed.

Pseudisograptus bellulus sp. nov.

Plate 26, fig. 8; text-fig. 21

Diagnosis. Pseudisograptus with the general size and shape of *P. hastatus*, but with a ventrally expanding manubrium, reaching about 2·2 mm wide at the base; simple prothecal folds present.

Holotype. NIGP 84735, from the Ningkuo Formation, Fentoushan, near Jiangshan, Zhejiang Province, China; the only available specimen, preserved in full relief in pyrite as an internal mould in reverse aspect.

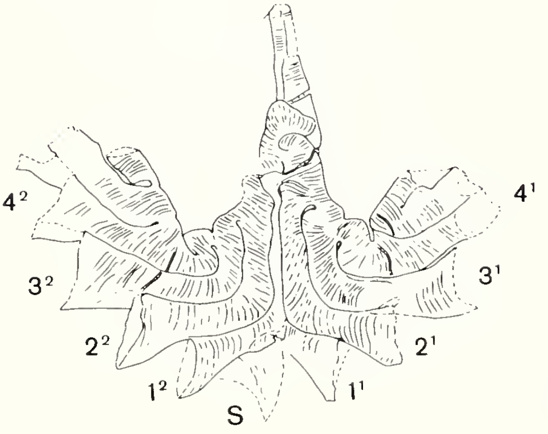
Horizon. Bed 11 in the Fengzou section, Fentoushan, measured by Han Nairen *et al.* (1984). It is associated with *P. m. janus*, *Didymograptus hirundo*, *Cardiograptus amplus*, and *Pseudotrigonograptus ensiformis*, and represents the *C. amplus* Zone, equivalent to upper Yapeenian.

Name. Bellulus, elegant.

Description. The rhabdosome has the general size and shape of the earlier *P. hastatus*. The sicula is at least 5·2 mm long with a free proximal portion of at least 1·2 mm. The manubrium is 1·6 mm long, has concave shoulders, and expands towards its base, reaching 2·2 mm wide. The shoulders have an undulating profile resulting from prothecal folding.

Only the proximal portions of the stipes are preserved, and they measure 1.9 mm in width. Stipe divergence angle is 300°.

Development is of dextral mode and isograptid type. The exact point of origin of th1^1 on the sicula cannot be seen but is at or near the top of the preserved portion of the sicula in our single specimen (text-fig. 21). Th1^2 arises on the reverse side of th1^1, at least 1·2 mm down and, as in *P. m. janus*, grows up and across to the stipe^2 side of the rhabdosome before commencing its downward growth. Th2^1 arises in similar fashion to that in *P. m. janus*, growing down for 2·2 mm and completely overlapping th1^1 before turning sharply outwards. Th3^1 and th4^1 have weak prothecal folds; th4^1 makes a sharp flexure to commence upward growth of the stipes. On the stipe^2 side, th2^2 grows down symmetrically opposite to th3^1 and partially overlaps the preceding th1^2.



TEXT-FIG. 21. *Pseudisograptus bellulus* sp. nov., holotype, NIGP 84735 from the Ningkuo Formation, Fentoushan, near Jiangshan, China, in full relief (internal mould), × 15.

Th2^2, th3^2, and th4^2 all appear to have weakly developed prothecal folds; th4^2, like its counterpart th4^1, makes the sharp upward flexure to commence upward stipe growth.

Compared with *P. m. janus* and *P. m. texanus*, relatively few thecae of the two thecal series overlap each other, and only the sicula, th1^1, and th1^2 show the plaited arrangement characteristic of *Pseudisograptus*. As in *P. m. janus* and *P. m. manubriatus*, but unlike *P. m. texanus*, the two thecal series do not overlap each other in the proximal region, their line of junction being represented by the contact between th1^2 and th2^1, approximately in the bilateral plane of the rhabdosome.

Discussion. Although only a single specimen is available, it is preserved in full relief with good growth lines, and proximal development and structure are clearly portrayed. The species in outline form most closely resembles *P. hastatus* from the early part of the upper Castlemainian, Ca3. It differs in the expanding manubrium which reaches a width considerably greater than that reached by *P. hastatus*. In the attitude of its proximal thecae, however, it more closely matches the smaller *P. gracilis* from the upper Ca3, inferred to be its nearest relative. Nothing is known of its range of morphologic variation. Because the probability of *P. bellulus* belonging to either *P. gracilis* or *P. hastatus* is in both cases less than 0·001 (using the *t*-test on manubrium width), it is here regarded as a distinct species.

Pseudisograptus gracilis (Ruedemann, 1947)

Text-fig. 22A–E

1947 *Isograptus caduceus* var. *gracilis* Ruedemann, p. 351, pl. 57, figs. 15 and 16.
1973 *Isograptus hastatus* Harris, Form B, Cooper, pp. 82–84, text-fig. 20*a–e* (*non* text-fig. 20*f–l*).
1979 *Pseudisograptus hastatus* (Harris), Form B, Cooper, p. 78, pl. 14, figs. *i*, *k*; text-fig. 59*a*, *b*.

Measured material. Eighteen specimens: VG 94, 95, 152, 156, 158; PR 282, 289, 300, 307, 310, 424, 583–588, and several incomplete specimens, from loc. S2/f552 of Cooper (1979, p. 99), Aorangi Mine track, north-west Nelson, New Zealand.

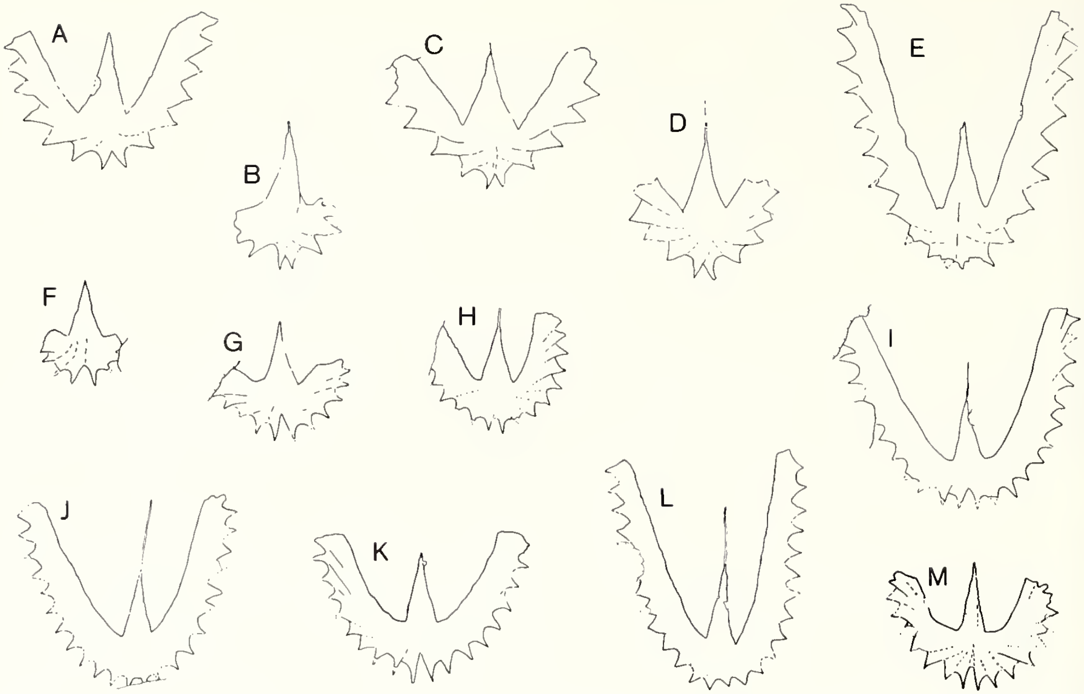
Horizon. Castlemainian *I. v. maximodivergens* Zone in New Zealand, equivalent to the upper part of Ca3 in Victoria.

Description. The rhabdosome is of smaller overall size than that of *P. hastatus* and has straighter stipes. Sicula length averages 3·7 mm (range 3·4–4·3 mm) and is 0·6 mm wide at the aperture. The manubrium averages 1·3 mm (range 0·7–1·8 mm) in width. Although in several specimens a distinct break in slope below the sicula apex can be seen, the top of the manubrium cannot be determined in many specimens in which the outline of the free proximal portion of the sicula and first theca passes smoothly into the manubrium. Supradorsal sicula length averages 2·1 mm, i.e. just over half the length of the sicula. The manubrium comprises the proximal portions of at least the first three pairs of thecae beyond th1^1, but details of its structure are unknown. From traces of the interthecal septa (see Cooper 1973, text-fig. 20*d*) it is likely that the two thecal series are symmetrically arranged about the bilateral plane rather than being superposed on each other as in *P. m. texanus*. The apertural portions of proximal thecae are directed away from the rhabdosome midline more strongly than in *P. hastatus*.

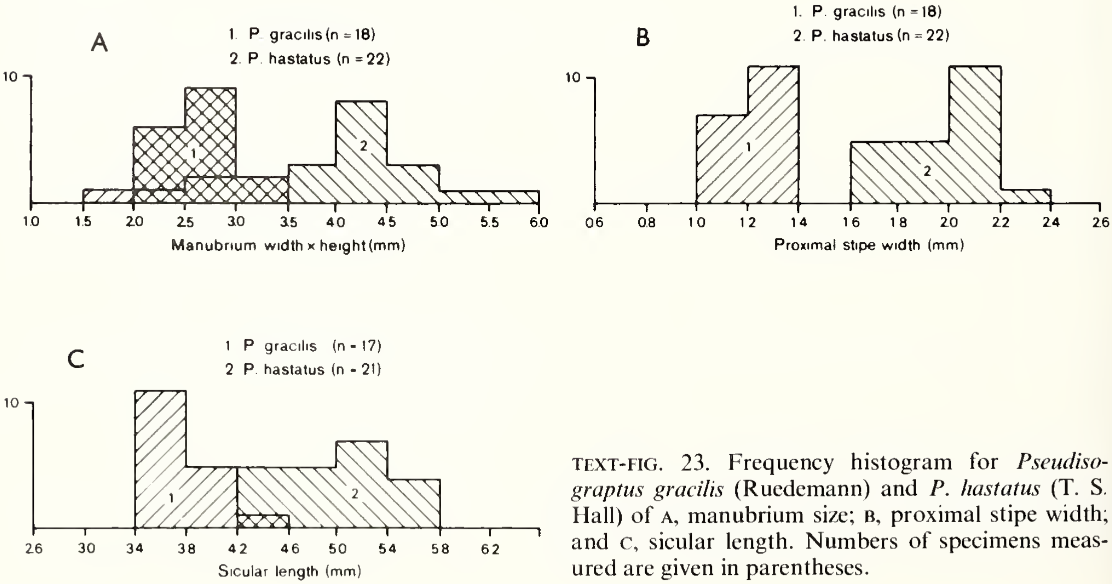
Stipes are short, up to 6 mm long, and bear no more than nine or ten thecae after their point of proximal flexure. They average 1·2 mm (range 1·0–1·3 mm) in width proximally and are generally parallel sided. Thecae are spaced about 3·3 in 3 mm and, like *P. hastatus*, lack a ventral apertural process.

Discussion. The species is erected for those forms referred to as *I. hastatus* Form B by Cooper (1973, 1979). Ruedemann's *I. caduceus* var. *gracilis* from the Glenogle shale of British Columbia closely matches the New Zealand material, although unfortunately the precise stratigraphic horizon was not given. Ruedemann's name, *gracilis*, thus appears to be the oldest available name for the species.

The species most closely resembles *P. hastatus* with which it was formerly included. Both possess a prominent wedge-shaped 'manubrium' and overlap in the range of several of their measured characters, particularly in dimensions of the 'manubrium' (text-fig. 23A) and stipe divergence angle. From the larger samples of the two forms now available, *P. gracilis* is most readily distinguished from *P. hastatus* by its narrower stipes (text-fig. 23B) and outwardly directed apertures of proximal

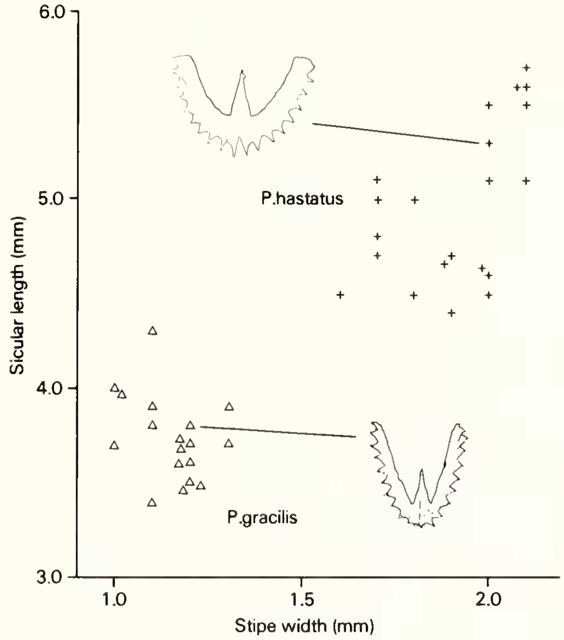


TEXT-FIG. 22. *Pseudisograptus gracilis* (Ruedemann) and *P. hastatus* (T. S. Hall). A–E, *P. gracilis*, from the upper Castlemainian Ca3 Zone, Aorangi Mine Track, north-west Nelson, New Zealand: A, VG 152; B, growth stage, PR 424; C, PR 584; D, immature specimen, PR 307; E, mature rhabdosome, VG 94. F–M, *P. hastatus*, from the lower Castlemainian Ca3 Zone, Anthill Creek, north-west Nelson, New Zealand (locality details in Cooper 1973): F, growth stage, PR 605; G, immature rhabdosome, PR 608; H, PR 120; I, PR 615; J, PR 124; K, PR 613; L, PR 118; M, specimen with traces of interthecal septa, PR 122. A–E, × 5; F–M, × 3.



TEXT-FIG. 23. Frequency histogram for *Pseudisograptus gracilis* (Ruedemann) and *P. hastatus* (T. S. Hall) of A, manubrium size; B, proximal stipe width; and C, sicular length. Numbers of specimens measured are given in parentheses.

thecae. When sicula length is plotted against stipe width (text-fig. 24), two clear groups result; on the PCA plot the two species form clearly distinguishable groups with non-overlapping fields (text-fig. 25), agreeing with the reclassification test which made no change to the original specific assignment. There seems little doubt that *P. gracilis* was derived from the earlier *P. hastatus*.



TEXT-FIG. 24. Sicular length plotted against stipe width for thirty-nine specimens of *Pseudisograptus gracilis* (Ruedemann) and *P. hastatus* (T. S. Hall).

Pseudisograptus hastatus (Harris, 1933)

Text-fig. 22F–M

1914 *Didymograptus caduceus manubriatus* T. S. Hall (*pars*), pl. 17, fig. 13.
1933 *Isograptus hastatus* Harris (*pars*), p. 104, text-figs. ?33, 34–36.
1973 *Isograptus hastatus* Harris, Form A, Cooper, pp. 82–84, text-fig. 20*f–l* (*non* text-fig. 20*a–e* = *Pseudisograptus gracilis*).
1979 *Pseudisograptus hastatus* (Harris), Form A, Cooper; Cooper, p. 78, text-fig. 59*c*, *d*.

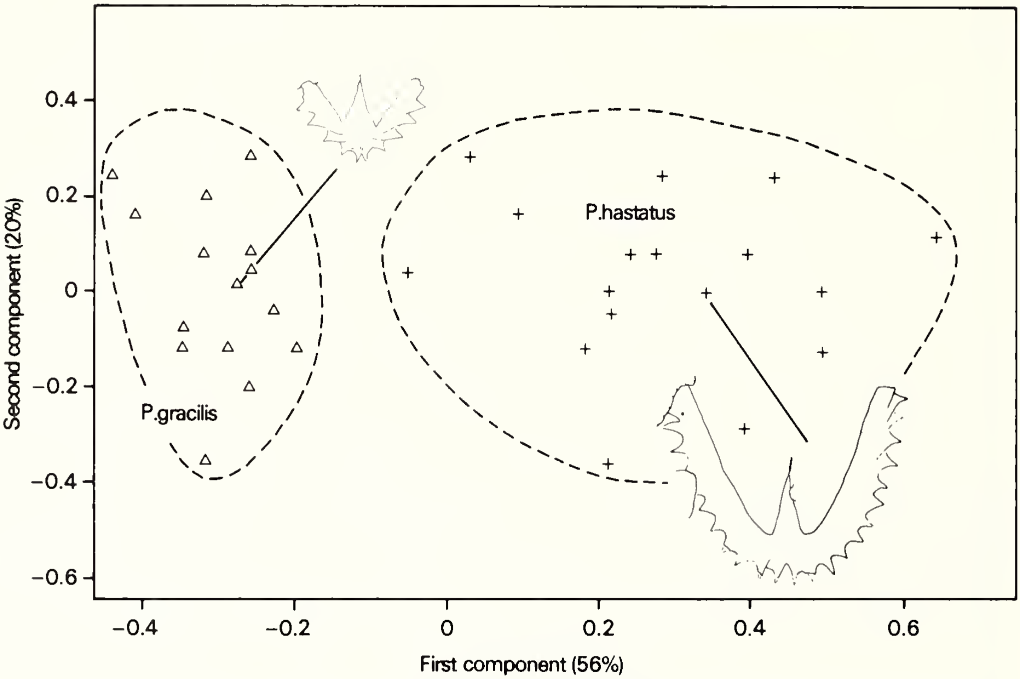
Holotype. GSV 63654, Museum of Victoria, figured by Harris (1933, text-fig. 36) and refigured by Cooper (1973, text-fig. 20*k*). Type locality is 'Sandy Creek Road near Bagshot, Bendigo'.

Measured material. Twenty-two specimens: PR 114, 116, 118–122, 124–127, 166, from loc. S2/f565 of Cooper (1979, p. 100); PR 602, 609, 613, 616, from loc. M25/f49; PR 603, 608, 611, 615, from loc. M25/f50; PR 605–607, from loc. M25/f51; all in Anthill Creek, Aorangi Mine area, north-west Nelson, New Zealand.

Horizon. Uppermost part of Castlemainian *lunatus* Zone in New Zealand, equivalent to the lower part of Ca3 in Victoria.

Description. The rhabdosome is comparable in size and, except for its manubrium, in shape to small members of the co-occurring *Isograptus victoriae maximus* population. The sicula averages 4·9 mm (range 4·4–5·7 mm) in length. There is no clearly defined free proximal portion of the sicula, as in later pseudisograptids; the apex passes smoothly into the shoulders of the manubrium. The height of the manubrium cannot therefore be determined, but its width is rather variable, averaging 1·4 mm (range 1·1–1·8 mm; $V = 14$). Supradorsal length of the sicula averages 2·7 mm (range 2·2–3·2 mm), i.e. about half the overall length of the sicula. The manubrium comprises the proximal portions of at least the first two pairs of thecae beyond th1^1, but details of its structure are unknown. Proximal thecae are relatively straight, and their apertural portions are directed away from the rhabdosome midline less strongly than in all subsequent pseudisograptid species.

Stipes reach 9 mm in length, average 1·9 mm (range 1·6–2·2 mm) in proximal width, and diverge at about 310° (range 285–330°). They taper gradually throughout their length and are curved proximally before becoming straight distally, giving the rhabdosome a rounded rather than V-shaped proximal outline. Thecae are spaced about 5·5 in 5 mm; their apertures are inclined at a high angle, giving deep 'thecal excavations', and are simple, not extended into a ventral process as in *P. manubriatus*.



TEXT-FIG. 25. PCA plot of specimens of *Pseudisograptus gracilis* (Ruedemann) and *P. hastatus* (T. S. Hall) from Aorangi Mine, north-west Nelson, New Zealand (locality details in Cooper 1973).

Discussion. Specimens grouped informally by Cooper (1973, 1979) as *I. hastatus* Form A are here given full specific status. They include forms which closely match Harris's holotype (see Cooper 1973) and are particularly interesting as they apparently represent the earliest known manubriate species, and are presumed to be ancestral to the manubriate stock. Although a larger sample population is available for study, little is known of the early development of the rhabdosome or of its proximal structure. However, the manubrium, judging from its size, is well developed.

Of the four specimens figured by Harris, three (his text-figs. 34–36) are from the upper Castlemainian, Ca3, and match the New Zealand specimens from the equivalent beds (upper part of *I. v. lunatus* Zone). One specimen (his text-fig. 33) is from the Yapeenian (loc. Ba71) and represents a growth stage. Because the age would be anomalous and the figure (at × 1) does not allow critical assessment, inclusion of the specimen in the species is here queried. So far as is known, *P. hastatus* is confined to the lower part of Ca3.

The distinction from *P. gracilis* is discussed under that species. From *P. manubriatus s.l.* it is distinguished by the lack of a break in slope at the top of the manubrium, its relatively straight proximal thecae, the lack of a thecal ventral apertural process, and a generally more isograptid appearance.

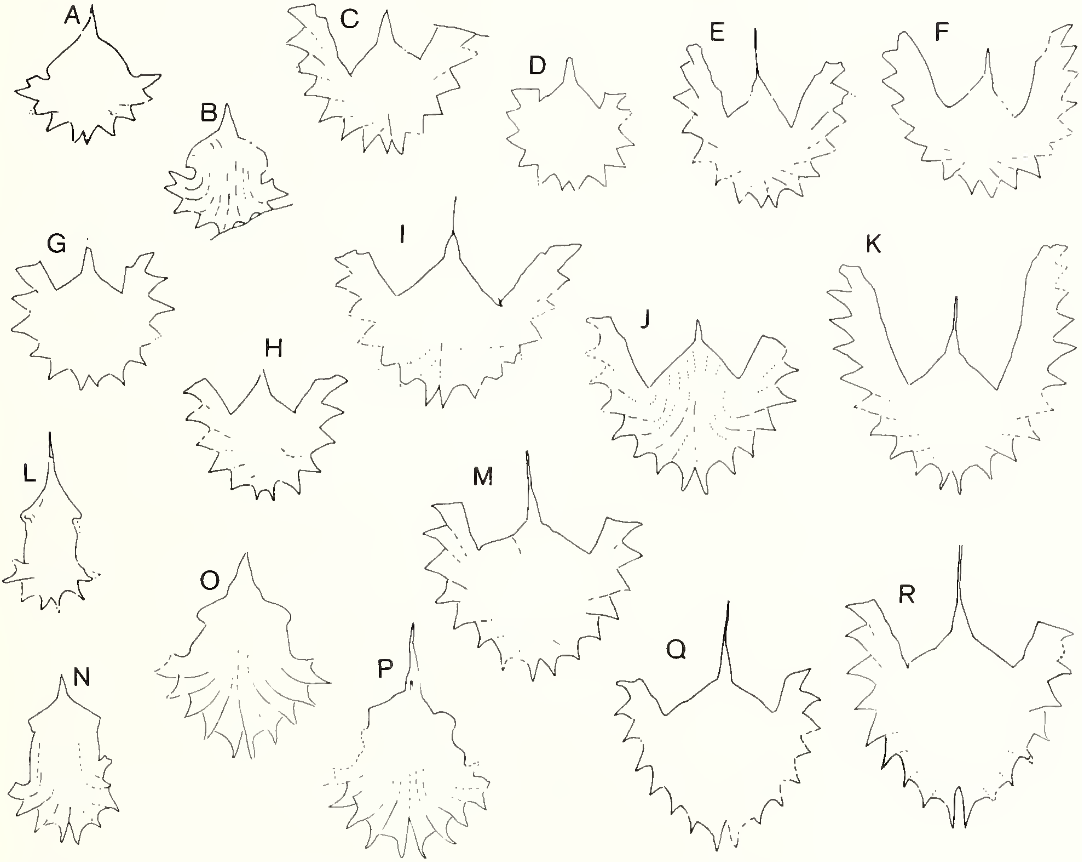
Pseudisograptus dumosus (Harris, 1933)

Plate 25, figs. 2 and 7; text-fig. 26A–K

1933 *Isograptus dumosus* Harris, p. 94, pl. 6, fig. 2*a–c*; text-figs. 37–39.
1933 *Isograptus caduceus velata* Harris, pp. 93–94, text-fig. 40.
1973 *Isograptus dumosus* Harris, Forms A and B, Cooper, pp. 78–82, text-fig. 18*e–p* (*non* text-fig. 18*a–d* = *P. jiangxiensis* Yu and Fang).
1979 *Pseudisograptus dumosus* (Harris), Forms A and B, Cooper; Cooper, pp. 77–78, pl. 14, figs. *g*, *h*; text-fig. 58*c–f*.

Lectotype. GSV 63651 in the Museum of Victoria, nominated and figured by Cooper (1973, p. 78, text-fig. 18*o*). Type locality is 'Ba71, Gisborne Creek', Victoria.

Measured material. Form A, twenty-two specimens: VG 89, 140; PR 27, 280, 281, 306, 423, 429, 432–434, 587–589, 591–597, and 599, all from loc. S2/f552 of Cooper (1979, p. 99), Aorangi Mine Track, north-west



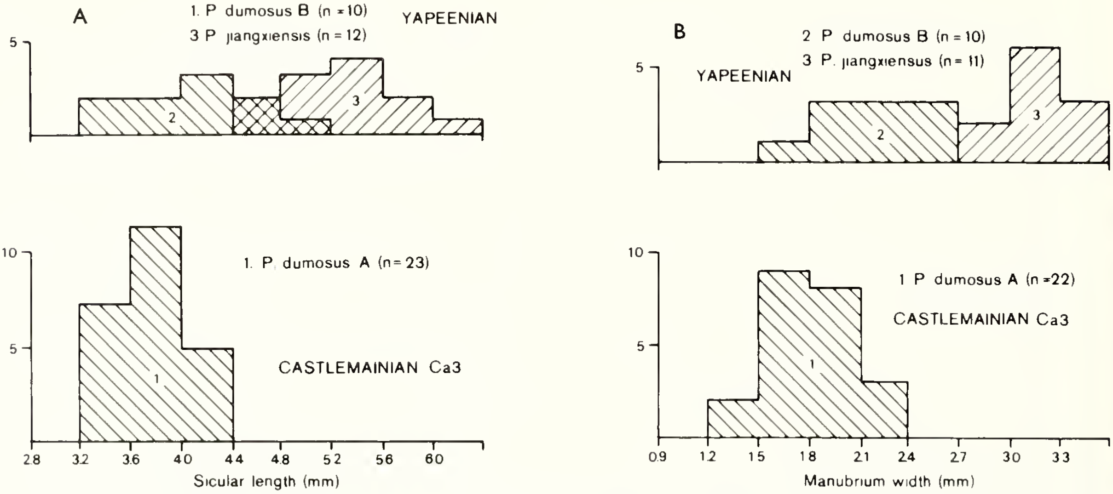
TEXT-FIG. 26. A–K, *Pseudisograptus dumosus* (Harris). A–F, Form A, from the Castlemainian Ca3 Zone, Aorangi Mine Track, north-west Nelson, New Zealand (locality details in Cooper 1973): A and B, immature rhabdosomes, PR 598 and PR 590; C, PR 433; D, PR 429; E, PR 594; F, PR 591. G–K, Form B, from the Yapeenian of Jimmy Creek, north-west Nelson, New Zealand, except for I which is from Willey's Quarry, Victoria: G, PR 412; H, PR 413; I, P 103885; J, PR 28; K. PR 414. L–R, *Pseudisograptus jiangxiensis* (Yu and Fang), from the Yapeenian of Jimmy Creek, north-west Nelson, New Zealand: M, PR 559a; N, advanced growth stage, PR 564; O, PR 366; P, PR 369; Q, PR 600; R, PR 384. All × 5.

Nelson, New Zealand. Form B, ten specimens: PR 28, 42, 315, 316, 339, 353, 374, 377, 412–415, from loc. S2/f540 of Cooper (1979, p. 97), Jimmy Creek, north-west Nelson, New Zealand.

Horizon. Castlemainian *maximodivergens* Zone in New Zealand, equivalent to the upper part of Ca3 in Victoria; and *Oncograptus* Zone, Yapeenian.

Description. Two informal forms are recognized: Form A from the *maximodivergens* Zone (upper Ca3) and Form B from the *Oncograptus* Zone (Ya).

The rhabdosome of Form A is small and compact with stipes barely developed beyond the manubrium. The sicula averages 3·7 mm (range 3·3–4·1 mm) in length. The apex of the sicula and first theca protrude about 1 mm above the manubrium which expands rapidly to a basal width averaging 1·7 mm (range 1·4–2·1 mm). The manubrium averages only 1·4 mm (range 1·0–1·6 mm) in length and is thus relatively broad and squat. The stipes are generally comprised of fewer than four thecae each and average 1·1 mm (range 0·8–1·5 mm) in width; they diverge at about 314° (range 270–340°). The ventral margin of the rhabdosome is rounded. Width of the rhabdosome at the level of the base of the manubrium is 4·1 mm (range 3·0–4·8 mm).

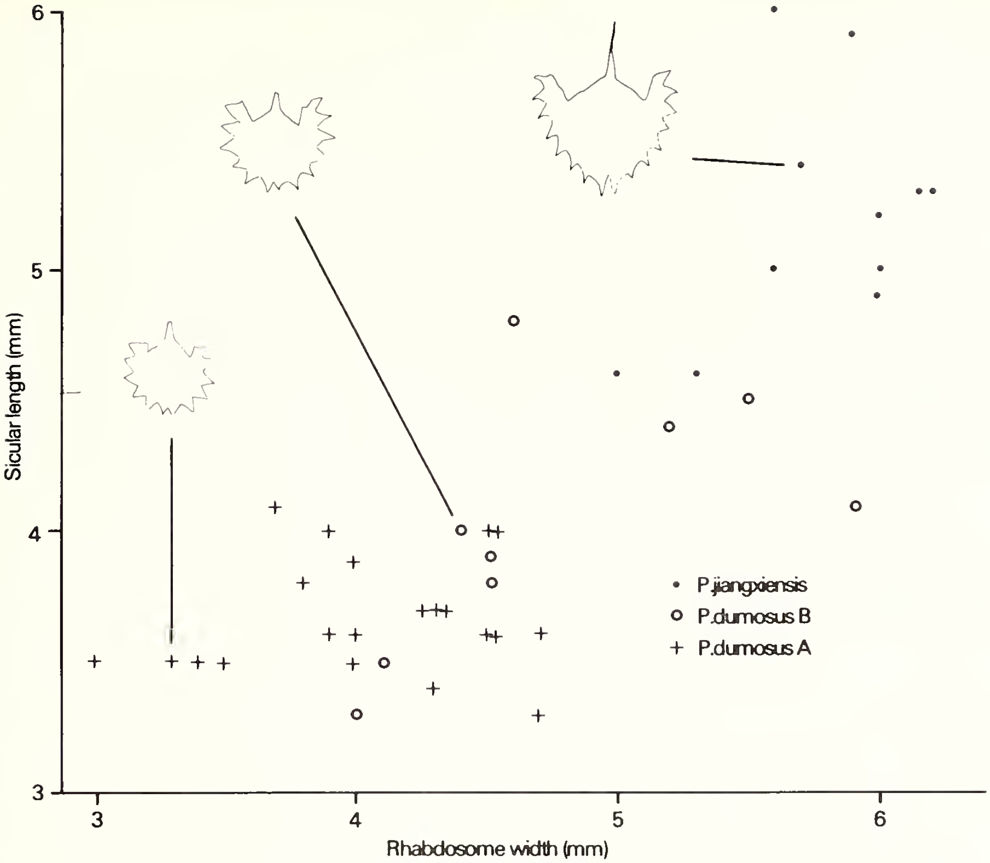


TEXT-FIG. 27. Frequency histograms for *Pseudisograptus dumosus* (Harris) Forms A and B, Cooper and *P. jiangxiensis* (Yu and Fang) of A, sicular length and B, manubrium width. Number of specimens measured are given in parentheses.

Form B has slightly larger overall rhabdosome dimensions with longer stipes bearing up to six thecae each. The sicula averages 4·0 mm (range 3·3–4·8 mm) in length; the manubrium averages 2·1 mm (range 1·7–2·4 mm) in width and 1·4 mm (range 1·1–1·6 mm) in length and has similar squat proportions to that of Form A. Stipe width is similar but rhabdosome width is appreciably wider, averaging 4·7 mm (range 4·0–5·9 mm).

Traces of interthecal septa can be seen in a few specimens of each form (text-fig. 26A–K) and show that the two thecal series were symmetrically arranged about the plane of bilateral symmetry as in other Australasian *Pseudisograptus* species.

Discussion. Specimens of *P. dumosus* from the upper Ca3 Zone in New Zealand were informally designated Form A by Cooper (1973, 1979) and those from the *Oncograptus* Zone (Yapeenian) Form B. Although the mean values of most of the measured characters are appreciably different in the two forms, there is considerable overlap in range of all characters (text-figs. 27 and 28). On the PCA plot (text-fig. 29) there is also considerable overlap of the fields of the two forms and this is reflected in the reclassification test: seven of the twenty specimens of Form A were reclassified in Form B, and one of the eight specimens of Form B was reclassified in Form A. Because of this relatively high proportion of reassigned specimens it is unwise to recognize the forms as distinct subspecies. The two forms have biostratigraphic value and are retained here as intraspecific informal



TEXT-FIG. 28. Sicular length plotted against rhabdosome width for forty-one specimens of *Pseudisograptus dumosus* (Harris) Forms A and B, Cooper and *P. jiangxiensis* (Yu and Fang), from the Upper Castlemainian and Yapeenian of Aorangi Mine, north-west Nelson, New Zealand.

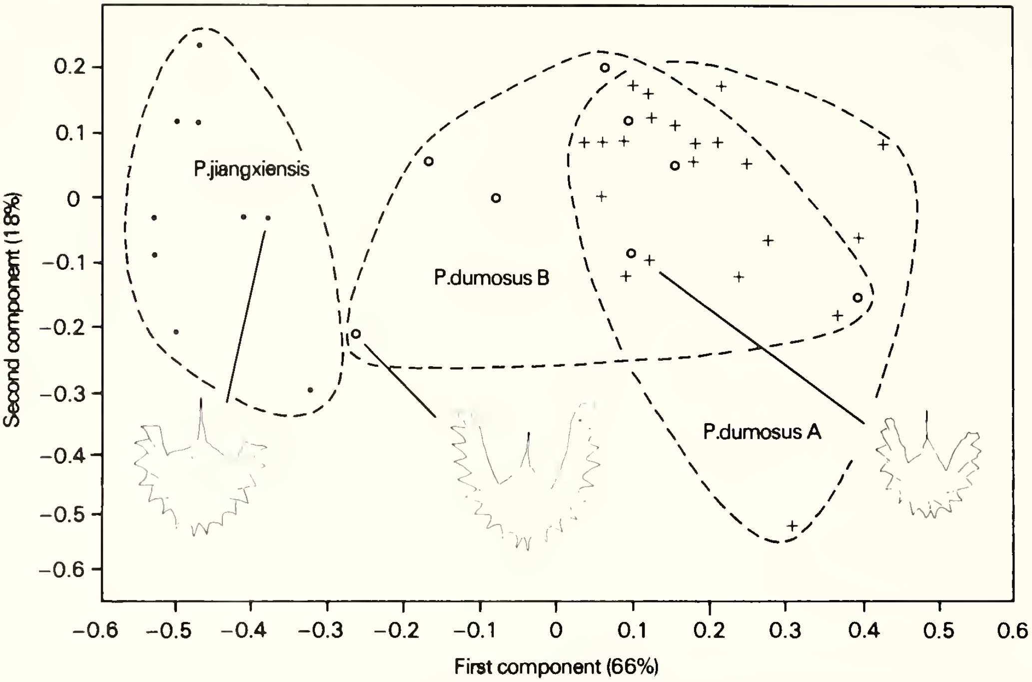
groups. The specimens described and figured by Harris (1933), including the lectotype (Cooper 1973, text-fig. 18*o*), most closely match Form A, but are from the Yapeenian of Victoria and may represent the smaller end of the Form B range.

Harris erected the variety *Isograptus caduceus* var. *velata* with a minimum of description and only one figure (at natural size). He grouped it with the manubriate species, especially with *P. dumosus* (Harris 1933, p. 105). Although few details can be seen in his figure, the form of the rhabdosome matches well with Form B (text-fig. 26K) and the variety is here synonymized accordingly. The specimens figured by Tsai (1974, pl. 9, figs. 8, 9) as *I. manubriatus* from the *I. gibberulus* (*I. victoriae*) Zone of Kazakhstan more closely match *P. dumosus* Form B and are here included in the species.

Pseudisograptus jiangxiensis (Yu and Fang, 1981)

Plate 25, figs. 1 and 6; text-fig. 26L–R

1973 *Isograptus dumosus* Harris, Form C, Cooper, pp. 78–82, text-fig. 18*a–d* (*non* text-fig. 18*e–p*).
1979 *Pseudisograptus dumosus* (Harris), Form C, Cooper; Cooper, pp. 77–78, text-fig. 58*a*, *b*.
1981 *Arienograptus jiangxiensis* Yu and Fang, pp. 29–30, pl. 1, figs. 1, 2; text-fig. 3.
1981 *Arienograptus zhejiangensis* Yu and Fang, pp. 30–31, pl. 1, figs. 3, 4; text-fig. 4.



TEXT-FIG. 29. PCA plot of specimens of *Pseudisograptus dumosus* (Harris) Forms A and B, Cooper, with widely overlapping fields, and *P. jiangxiensis* (Yu and Fang) with a discrete field of morphology.

Measured material. Twelve specimens: PR 315, 338, 366, 384, 400, 410, 425, 538, 559, 575, 600, and 601, from loc. S2/f540 of Cooper (1979, p. 97), Jimmy Creek, north-west Nelson, New Zealand.

Horizon. Yapeenian, lower *Oncograptus* Zone in New Zealand, equivalent to Ya1 in Victoria. The species was described from the *Glyptograptus austrodentatus* Zone and *Cardiograptus amplus* Zone of the Ningkuo shale.

Description. The rhabdosome is composed of little more than an enlarged manubrium; its outline is like that of *P. dumosus* but is more massive and 'deeper', with a greater distance between the base of the manubrium and ventral rhabdosome margin and relatively shorter stipes. There are twelve thecal apertures in the infradorsal ventral margin whereas in *P. dumosus* (both Form A and Form B) there are only nine or ten. The sicula and th1^1 protrude slightly, giving a rather pointed outline to the ventral margin rather than a smoothly rounded curve as in *P. dumosus*.

The sicula averages 5·2 mm (range 4·6–6·0 mm) in length and, as in th1^1, its ventral margin is extended into a denticle-like process. Its free proximal portion is 1–2 mm long, generally about 1·3 mm. Ventrally concave recurvature of the distal portions of proximal thecae is more marked than in *P. dumosus*, and imitates the *caduceus* condition. The manubrium is broader than that of *P. dumosus* (text-fig. 27B) and expands more rapidly; it averages 3·1 mm (range 2·8–3·3 mm) in width and 1·5 mm (range 1·2–1·7 mm) in length. Manubrium structure is unknown but traces of interthecal septa in some specimens (text-fig. 26N–P) suggest that, as in *P. dumosus*, the two thecal series lie symmetrically to either side of the rhabdosome's plane of bilateral symmetry.

Stipes are short and possess only two or three thecae each beyond the base of the manubrium. They average 1·3 mm (range 1·1–1·5 mm) in width and diverge at about 322° (range 305–330°).

Discussion. The Nelson material was originally described informally as *P. dumosus* Form C by Cooper (1973, 1979). The distinction from *P. dumosus* has been outlined in the description above. Apart from the differences in rhabdosome shape, the wider manubrium serves to distinguish *P. jiangxiensis* from *dumosus*. On the PCA plot (text-fig. 29) *P. jiangxiensis* forms a group distinct from *P. dumosus* and the reclassification test made no changes to the original assignment. Although we have only a comparatively small sample to go by, there seem good grounds for the recognition of the specimens as a distinct species. The species is confined to the lower Yapeenian, in the same beds as *P. dumosus* Form B.

Yu and Fang (1981) erected the genus *Arienograptus* with *A. jiangxiensis* as type species. Their figures show an incompletely developed rhabdosome that, allowing for the different modes of preservation, matches well with growth stages from Nelson (text-fig. 26L–P). The main point of difference concerns the growth paths of proximal thecae; the Chinese specimens are all preserved in reverse view, whereas at least one of the Nelson specimens (text-fig. 26P) shows the obverse view. We therefore regard the Nelson specimens as belonging to Yu and Fang's species and their genus *Arienograptus* as a junior synonym of *Pseudisograptus*. Their species *A. zhejiangensis* is a later growth stage, closely matching Nelson specimens (e.g. Cooper 1973, text-fig. 18C) and is synonymized accordingly. Their account of proximal development has th1^2 budding off th2^2 before th2^1; if correct, this would be unique among the dichograptids. Unfortunately, the feature cannot be verified from their published illustrations.

NOTES ON OTHER MANUBRIATE SPECIES

Pseudisograptus tau (Harris, 1933)

The species *Maeandrograptus tau* Harris is clearly morphologically related to *P. manubriatus koi*, particularly those variants with wide open rhabdosomes and loss, or partial loss, of isograptid symmetry (text-fig. 12D). *P. tau* seems to have gone a stage further and has acquired maeandrograptid symmetry; the rhabdosome's midline passes through the sicula in specimens figured by Cooper (1973, text-fig. 24*b*, *d*). The species has a prominent manubrium and is therefore excluded from *Maeandrograptus* Moberg and included here in *Pseudisograptus*. Harris (1933) gives the horizon as Yapeenian—the species is found together with *P. m. manubriatus* at Willey's Quarry, Ya2.

Pseudisograptus? *aggestus* (Harris, 1933)

Harris based this species on two specimens from the upper Castlemainian at Yandoit. The holotype was refigured by Cooper (1973); although the stipes are undeveloped (or broken off), the distal portions of proximal thecae have lower inclination than in other manubriate species and are somewhat crowded in the proximal region. If the New Zealand specimens (text-fig. 30A, B) are correctly assigned to the species, then a more advanced growth stage is available for study. The stipes are barely reclined, 2·1 mm wide and reach 4·4 mm long. Thecae are long and narrow, of very low inclination, and of manubriate type. The manubrium is weakly developed, 0·6 mm long, and 1·5–2·0 mm wide. The free proximal portion of the sicula and first theca protrude 1·0–1·3+ mm above the top of the manubrium. Isograptid symmetry is weak or lacking altogether.

TEXT-FIG. 30. A and B, *Pseudisograptus*? *aggestus* (Harris) from the upper Castlemainian Ca3 (*I. v. maximodivergens* Zone) of Aorangi Mine Track, north-west Nelson, New Zealand (locality S2/f522 of Cooper 1973). Two specimens thought to represent the mature rhabdosome of the species otherwise known only from the immature holotype: A, PR 570; B, PR 569. Both ×5.

Because it has a manubrium the species is precluded from *Maeandrograptus* Moberg. It is morphologically closest to *P.*? *geniculatus* (Skevington), the two species sharing a weakly developed manubrium and stipes that are barely reclined. *P.*? *geniculatus* has good isograptid symmetry, however, and its proximal thecae are more highly inclined. The inclusion of *aggestus* in *Pseudisograptus* would presume that the lack of good isograptid symmetry is a secondary loss feature, as in *P. tau*. The species can be less certainly linked with other *Pseudisograptus* species, however, and its generic reference is less certain. It is confined to the upper Castlemainian, Ca3.

Pseudisograptus? *geniculatus*

With its barely reclined stipes and weakly developed manubrium, this species at first sight does not look much like other manubriate species. Its proximal structure can be interpreted as manubriate (text-fig. 1B) and this feature, together with the form of its thecae and presence of prothecal folds, is the basis for its tentative inclusion in *Pseudisograptus*. The species is known from the *D. hirundo* Zone of Öland (Skevington 1963, pp. 67–70).

British pseudisograptids

In his revision of the isograptids of England and Wales, Jenkins (1982) referred a number of species to *Pseudisograptus*. His *P.*? *menaiensis* and the similar *P. angel* include the only comparatively well-preserved material; they differ from the Australasian species in possessing a barely developed manubrium, and thecae (particularly in the proximal part of the stipes) of relatively high inclination. As recognized by Jenkins, *P.*? *menaiensis* is reminiscent of isograptids of the *caduceus* group, but it has a much longer sicula and proximal thecae than in any *caduceus* group form; this feature, together with the sigmoidal curvature of proximal thecae and the weakly developed manubrium, suggest that both *P.*? *menaiensis* and *P. angel* are pseudisograptids. The British species, together with *P.*? *geniculatus*, however, appear to form a distinct European group which may, as Jenkins pointed out, have been independently derived and not belong to *Pseudisograptus* at all. Until more is known of these British forms, they are tentatively retained within *Pseudisograptus*, following Jenkins.

The forms described by Jenkins as *P. stella*, *P.* n. sp. A, and *P.* n. sp. B are either too poorly preserved or too fragmentary to allow their morphologic affinity with other species to be assessed.

COMMENTS ON RELATED GENERA

Apiograptus and *Exigraptus*

On the basis of its generally isograptid symmetry and similarities in development and thecal morphology, *Apiograptus* Cooper and McLaurin, 1974 was regarded by its authors as being most closely linked with *Pseudisograptus*, particularly with *P. m. janus* (formerly *P. manubriatus* Form C). The biserial, incipiently monopleural rhabdosome can be derived from that of *P. m. janus* or a similar form by a continuation of the tendency of the dorsal stipe margin to grow around in a loop and recross the path of its earlier growth (Cooper and McLaurin 1974, pp. 82–83). Proximally, in material from Chinaman's Creek, Victoria, the stipes enclose the manubrium in pseudopericalycal fashion but distally they are apparently dipleural; two specimens of uncertain affinity described by Beavis (1962) from Bendigo, and which may represent the genus, have a monopleural distal stipe arrangement.

With its glossograptid thecal form, Harris and Thomas (1935) were led to include the type species, *A. crudus*, in *Glossograptus* albeit tentatively. Cooper and McLaurin pointed out (p. 75) that *Glossograptus* could only be derived from *Apiograptus* if there were a change from isograptid to dichograptid (= artus) development type and platycalycal to pericalycal mode. It is particularly interesting therefore that *G. ciliatus* from the Athens Shale described by Finney (1978, fig. 4) has dextral isograptid development differing from that generally accepted for Glossograptidae (Bulman 1970, fig. 62); further, its proximal structure is just what would be expected if the '*Apiograptus* trend' was continued a stage further; the base of the manubrium is defined by $th5^1$ instead of a later theca, and the second thecal series develops on the reverse side of the rhabdosome. The loop is right-handed, rather than left-handed as it appears to be in *Apiograptus*; in *P. m. janus*, however, the loop is either right- or left-handed and sense of rotation may not be significant.

On the other hand, the features linking *Apiograptus* with *P. manubriatus* (isograptid symmetry, similarity in development and in thecal morphology) are now known to be plesiomorphic (primitive) for the group which includes *Kalpinograptus* and the glossograptids and therefore are not useful for subdivision of the group. Although its proximal structure remains to be confirmed by the discovery of unflattened specimens, we feel

Apiograptus is best regarded as a sister group to the Glossograptina *sensu* Jaanusson (text-fig. 4), being distinguished from them by its less 'advanced' pseudopericalycal structure.

The genus *Exigraptus* Mu *in* Mu *et al.*, 1979, with *E. clavus* as type species, is closely similar to *Apiograptus*. The three differences cited by Mu *et al.* (1979, p. 164) are likely to be significant at the species level rather than genus level:

1. *Exigraptus* is dipleural. Monopleural stipe arrangement in *Apiograptus* applies only to the proximal region, as determined from the specimen figured by Cooper and McLaurin (1974, text-fig. 2*c*); distally the stipes appear to be in dipleural arrangement. It seems likely to us that there will be some variation in this character among species of the genus and that it will not be a reliable basis for generic distinction.
2. Maeandrograptid symmetry. The specimens of *A. crudus* figured by Cooper and McLaurin have proximal symmetry ranging from isograptid to maeandrograptid and in this feature resemble *P. manubriatus koi*. Proximal symmetry is thus not a diagnostic character.
3. Thecal flexure. Proximal thecae in *Exigraptus* are more sharply flexed than in *A. crudus* and there are fewer downwardly directed thecae; this seems to be the most significant point of difference. However, among the specimens from Chinaman's Creek figured by Cooper and McLaurin there is considerable variation in the number of downwardly directed thecae suggesting, again, that the Chinese material differs at the level of species rather than genus. There may well be a similar range of variation among Chinese material, as suggested by the slab figured by Chen (1982, pl. 1) which contains an array of forms ranging from those with wide rhabdosomes, rounded proximal ends, and many downwardly directed thecae, listed as *Exigraptus globosus* sp. nov. (surely conspecific with *A. crudus*), to those with narrower rhabdosomes and squarer proximal ends, listed as *E. clavus* Mu, *E. uniformis* Mu, *E. confertus* sp. nov., and *E. latus* sp. nov. (A population study is clearly needed to verify the presence of the five species as opposed to a single, variable population.)

For these reasons we think *Exigraptus* is best regarded as a synonym of *Apiograptus*.

Kalpinograptus and *Apoglossograptus*

Kalpinograptus Jiao, 1977, with *K. spiroptenus* as type species, is a manubriate form with a rhabdosome generally shaped like that of *P. manubriatus s.l.* It comes from the Saergan Formation of Kalpin, Xinjiang, where it is associated with *Nemagraptus exilis* and *Pseudoclimacograptus scharenbergi minor* and represents an interval considerably younger than that of the species discussed here. The structure of the first few thecae appears to be generally similar to that of *P. manubriatus*, but it is not clear from Jiao's diagrams or illustrations whether the sicula and first three thecae are platycalycal (as in *manubriatus*) or whether th1^2 wraps around the 'obverse' side of the sicula in a pericalycal fashion; from Jiao's figs. 5*a* and 5*b* it would appear that they are platycalycal. In any case, subsequent development differs from that of *manubriatus* in that the two thecal series develop on either side of the sicula, enveloping it and producing a pseudopericalycal structure as in *Glossograptus ciliatus* and *Cryptograptus marcidus* (Finney 1978).

The first thecal series expands across the sicula, th1^1, and th1^2 on the reverse side of the rhabdosome to form the manubrium; on the obverse side the manubrium is formed by the second thecal series. In *P. m. texanus*, the only pseudisograptid with comparable manubrial asymmetry, it is the other way round; the second thecal series expands across the sicula on the reverse side. *Kalpinograptus* thus shares affinities with the manubriate isograptids and the glossograptids.

From the Athens Shale of Alabama, Finney (1978) has described closely similar forms (but including more mature rhabdosomes) as *Isograptus lyra* Ruedemann, referring them to his new genus *Apoglossograptus* (a *nomen nudum*). Growth stages figured by Finney (1978, fig. 8*a–d*) show that the structure is pseudopericalycal; th1^2 grows around to that side of the sicula opposite th1^1, and does not overlap it on the reverse side as in pseudisograptids. The distinctive arrangement of stipes and the large proximal boss produced by overlapping thecae in the manubrium, as well as thecal morphology and rhabdosome shape, are features shared with *K. spiroptenus* and it seems most probable to us, on the basis of the published evidence by Jiao (1977) and Finney (1978), that the two are congeneric.

Origin of the glossograptids

Finney (1978) has shown that in at least two species of glossograptids (*G. ciliatus* and *Cryptograptus marcidus*) development is of isograptid type, thus demonstrating that development type in glossograptids is not exclusively of artus (= 'dichograptid') type (Bulman 1970). A case was also made for the reinterpretation of development type and mode in *G. holmi* and *C. tricornis*. Discussion of this problem is beyond the scope of this paper but we feel that Finney has established that artus development type is not likely to be a synapomorphy for the group, and that derivation from an ancestor with isograptid development type (the primitive state) is more likely. The derivation of artus type from isograptid type in other lineages has already been suggested (Cooper and Fortey 1983).

The two objections to the hypothesis of Harris and Thomas (1935) that the glossograptids were derived from the manubriate stock raised by Cooper and McLaurin (1974, p. 75), namely artus development and pericalycal structure, no longer apply, and the hypothesis is accepted here, at least as a working model. The glossograptids have, during their early development, an initially downward growth of proximal thecae (up to the third thecal pair in *G. ciliatus*) which can be regarded as homologous with that in pseudisograptids, supporting the hypothesis. Species such as *C. tricornis* (Bulman 1944; Finney 1978), where this initially downward growth is confined to the first two thecal pairs, would be interpreted as having partially lost the feature.

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REFERENCES

BEAVIS, F. C. 1962. *Glossograptus crudus* from the Bendigo East, Victoria. *Aust. J. Sci.* **24,** 485–486.

—— 1972. The manubriate isograptids. *Geol. Mag.* **109,** 193–204.

—— and BEAVIS, S. 1974. The Victorian isograptids and isograptid-like graptoloids. *Proc. R. Soc. Vict.* **86,** 175–213.

BERRY, W. B. N. 1960. Graptolite faunas of the Marathon Region, West Texas. *Publs Bur. econ. Geol. Univ. Tex.* **6005,** 129 pp., 20 pls.

BULMAN, O. M. B. 1945–1947. A monograph of the Caradoc (Balclatchie) graptolites from limestones in Laggan Burn, Ayrshire. *Palaeontogr. Soc.* (*Monogr.*), 70 pp., 10 pls. (1945, 1–42, pls. 1–3; 1946, 43–58, pls. 4–6; 1947, 59–78, pls. 7–10).

—— 1963. The evolution and classification of the Graptoloidea. *Q. Jl geol. Soc. Lond.* **119,** 401–418.

—— 1968. The mode of development of *Isograptus manubriatus* (T. S. Hall). *Geol. Mag.* **105,** 211–316.

—— 1970. Graptolithina. *In* Moore, R. C. (ed.). *Treatise on Invertebrate Paleontology, Part V* (2nd edn.), xxxii + 163 pp. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.

CARTER, C. and TAILLEUR, I. L. 1984. Ordovician graptolites from the Baird Mountains, Western Brooks Range, Alaska. *J. Paleont.* **58,** 40–57.

CHEN, X. 1982. Early Ordovician *Exigraptus* and *Glyptograptus* from Xingan, N. Guangxi and the origin of the biserial Axonophorous graptolites. *Acta palaeont. sin.* **21,** 505–514.

COOPER, R. A. 1973. Taxonomy and evolution of *Isograptus* Moberg in Australasia. *Palaeontology*, **16,** 45–115.

—— 1979. Ordovician geology and graptolite faunas of the Aorangi Mine area, north-west Nelson, New Zealand. *Palaeont. Bull. Wellington*, **47,** 127 pp., 19 pls.

—— and FORTEY, R. A. 1982. The Ordovician graptolites of Spitsbergen. *Bull. Br. Mus. nat. Hist.* (*Geol.*), **36,** 157–302.

—— 1983. Development of the graptoloid rhabdosome. *Alcheringa*, **7,** 201–221.

—— and LINDHOLM, K. 1984. The phylogenetic relationships of the graptolites *Tetragraptus phyllograptoides* and *Pseudophyllograptus cor*. *Geol. För. Stockh. Förh.* **106,** 279–291.

—— and MCLAURIN, A. N. 1974. *Apiograptus* gen. nov. and the origin of the biserial graptoloid rhabdosome. *Spec. Pap. Palaeont.* **13,** 75–86.

FINNEY, S. C. 1978. The affinities of *Isograptus*, *Glossograptus*, *Cryptograptus*, *Corynoides* and allied graptolites. *Acta palaeont. pol.* **23,** 481–495.

—— and CHEN, X. 1984. *Bergstroemograptus* n. gen. *crawfordi* (Harris) from the Ordovician of western Newfoundland. *Can. J. Earth Sci.* **21,** 1194–1199.

HALL, T. S. 1914. Victorian graptolites, Part IV; some new or little known species. *Proc. R. Soc. Vict.* **27,** 104–118.

HAN NAIREN, LI LUOZHAO and JIN YUSHU 1984. New observations on the Ningkuo Formation, Lower Ordovician, from Jiangshan, Zhejiang. *Jl. Guilin College Geol.* **4,** 1–8.

HARRIS, W. J. 1933. *Isograptus caduceus* and its allies in Victoria. *Proc. R. Soc. Vict.* **46,** 79–114.

—— and THOMAS, D. E. 1935. Victorian graptolites (New Series) Part III. Ibid. **47,** 288–313.

JAANUSSON, V. 1960. Graptoloids from the Ontikan and Viruan (Ordovician) Limestones of Estonia and Sweden. *Bull. geol. Instn Univ. Upsala*, **38,** 289–366.

JENKINS, C. J. 1982. *Isograptus gibberulus* (Nicholson) and the isograptids of the Arenig series (Ordovician) of England and Wales. *Proc. Yorks. geol. Soc.* **44,** 219–248.

JIAO, Q. 1977. *Kalpinograptus*, a new-graptolite from the Saergan Formation in Kalpin of Xinjiang. *Acta palaeont. sin.* **16,** 287–292.

LAPWORTH, C. 1873. On an improved classification of the Rhabdophora. *Geol. Mag.* **10,** 500–504, 555–560.

MU, A. T., GE, M. Y., CHEN, X., NI, Y. N. and YIN, Y. K. 1979. Lower Ordovician graptolites of southwest China. *Palaeont. sin.* **15,** 92–98.

ROSS, R. J. JUN. and BERRY, W. B. N. 1963. Ordovician graptolites of the Basin Ranges in California, Nevada, Utah and Idaho. *Bull. U.S. geol. Surv.* **1134,** 177 pp., 13 pls.

RUEDEMANN, R. 1947. Graptolites of North America. *Mem. geol. Soc. Am.* **19,** 652 pp., 92 pls.

SALTER, J. W. 1863. Note on Skiddaw Slate fossils. *Q. Jl geol. Soc. Lond.* **19,** 79–84.

SKEVINGTON, D. 1963. A correlation of Ordovician graptolite bearing sequences. *Geol. För. Stockh. Förh.* **85,** 298–319.

—— 1968. The affinities of *Oncograptus*, *Cardiograptus*, and allied graptolites from the Lower Ordovician. *Lethaia*, **1,** 311–324.

THOMAS, D. E. 1960. The zonal distribution of Australian graptolites. *J. Proc. R. Soc. N.S.W.* **94,** 1–58.

TSAI, D. T. 1974. *Graptolity Rannego Ordovika Kazakhstana.* Izdatel'stvo Nauka, Moscow.

WHITTINGTON, H. B. and RICKARDS, R. B. 1969. Development of *Glossograptus* and *Skiagraptus*, Ordovician graptoloids from Newfoundland. *J. Paleont.* **43,** 800–817.

WILEY, E. O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics.* John Wiley, New York.

YU, J.-H. and FANG, Y.-T. 1981. *Arienograptus*, a new graptolite genus from the Ningkuo Formation (Lower Ordovician) of South China. *Acta palaeont. sin.* **20,** 27–32.

—— —— 1983. In *Regional Palaeontology of Zhejiang Province*, 406–407.

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APPENDIX

The number of measured specimens (N), minimum value (Min), maximum value (Max), mean value (Mean), standard error of the mean (x), standard deviation (s), 95 % confidence limits (95 % c.l.), and coefficient of variation (V) are given below for each measured character of each species, together with the correlation matrix (coefficients significant at the 95 % level are underlined). The MINITAB program was used to generate these statistics.

Pseudisograptus hastatus

Measured character	N	Min.	Max.	Mean	s_x	s	95% C.l.	V	Correlation matrix 1	2	3	4
1 Sicular length	21	4.4	5.7	4.9	.09	.41	4.8-5.1	8				
2 Manubrium width	21	1.1	1.8	1.4	.04	.19	1.4-1.5	14	.420			
3 Supradorsal length	22	2.2	3.2	2.7	.07	.33	2.6-2.9	12	.675	.447		
4 Stipe divergence	18	285	330	312	3	15	305-319	4	.025	.239	-.267	
5 Proximal stipe width	22	1.6	2.2	1.9	.04	.17	1.9-2.0	8	.468	.498	-.046.	.456

Pseudisograptus gracilis

	N	Min.	Max.	Mean	s_x	s	95% C.l.	V	1	2	3	4
1 Sicular length	17	3.4	4.3	3.7	.056	.22	3.6-3.9	6				
2 Manubrium width	18	0.7	1.8	1.3	.05	.21	1.2-1.4	16	-.220			
3 Supradorsal length	18	1.8	2.6	2.1	.048	.20	2.0-2.2	10	.637	-.427		
4 Stipe divergence	16	270	340	306	5.2	21	295-317	7	-.153	.405	-.078	
5 Proximal stipe width	18	1.0	1.3	1.2	.018	.08	1.1-1.2	7	-.274	-.537	.013	-.132

Pseudisograptus dumosus form A

	N.	Min.	Max.	Mean	s_x	s	95% C.l.	V	1	2	3	4	5	6
1 Sicular length	23	3.3	4.1	3.7	.046	.22	3.6-3.8	6						
2 Manubrium width	22	1.4	2.1	1.7	.048	.23	.16-1.8	14	-.008					
3 Manubrium length	22	1.0	1.6	1.4	.037	.17	1.3-1.5	12	.431	.097				
4 Stipe divergence	15	270	340	314	7	25	328-300	8	-.255	.069	.335			
5 Proximal stipe width	21	0.8	1.5	1.1	.036	.17	1.0-1.2	15	.076	-.454	.000	.132		
6 Rhabdosome width	21	3.0	4.8	4.1	.11	.5	3.9-4.3	12	.083	.304	.587	.263	.218	

Pseudisogrptus dumosus form B

	N.	Min.	Max.	Mean	s_x	s	95% C.l.	V	1	2	3	4	5	6
1 Sicular length	10	3.3	4.8	4.0	.14	.45	3.7-4.3	11						
2 Manubrium width	10	1.7	2.4	2.1	.077	.25	1.9-2.3	12	.702					
3 Manubrium length	10	1.1	1.6	1.4	.047	.15	1.3-1.5	11	.478	.243				
4 Stipe divergence	7	285	345	316	10	26	292-339	8	-.663	-.560	.080			
5 Proximal stipe width	9	0.9	1.5	1.1	.057	.17	0.9-1.2	15	.472	.702	.067	.606		
6 Rhabdosome width	9	4.0	5.9	4.7	.23	.69	4.2-5.2	15	.566	.842	.364	-.205	.779	

Pseudisograptus jiangxiensis

		N.	Min.	Max.	Mean	s_x	s	95% C.l.	V	1	2	3	4	5	6
1	Sicular length	12	4.6	6.0	5.2	.13	.45	4.6-5.5	9						
2	Manubrium width	11	2.8	3.3	3.1	.052	.17	3.0-3.2	5	-.177					
3	Manubrium length	11	1.2	1.7	1.5	.049	.16	1.4-1.6	11	.428	-.447				
4	Stipe divergence	7	305	330	322	2.6	7	316-329	2	.970	-.430	.689			
5	Proximal stipe width	9	1.1	1.5	1.3	.035	.11	1.2-1.4	8.5	-.378	.371	-.450	-.351		
6	Rhabdosome width	10	5.0	6.2	.58	.11	.38	5.5-6.0	7	.401	-.409	.05	.015	.455	

Pseudisograptus manubriatus harrisi

		N.	Min.	Max.	Mean	s_x	s	95% C.l.	V	1	2	3	4	5	6
1	Sicular length	30	6.8	0.0	8.1	.13	.74	7.8-8.4	9						
2	Manubrium width	29	1.2	2.4	1.9	.06	.30	1.8-2.0	16	.190					
3	Manubrium length	29	1.0	3.0	2.1	.09	.51	1.9-2.3	24	.138	.417				
4	Free prox. length	29	1.0	4.0	2.1	.14	.73	1.9-2.4	35	.597	.141	-.200			
5	Stipe divergence	30	275	353	323	3	14	318-328	4	-.018	-.232	-.428	-.065		
6	Prox. stipe width	30	2.4	3.4	2.9	0.5	.26	2.8-3.0	9	.162	.377	.071	-.056	.192	
7	Distal stipe width	14	2.6	4.5	3.1	.14	.53	2.8-3.4	17	.024	.630	.304	-.028	.348	

Pseudisograptus manubriatus koi (Jimmy Creek)

		N.	Min.	Max.	Mean	s_x	s	95% C.l.	V	1	2	3	4	5	6
1	Sicular length	50	4.5	6.2	5.4	.055	.39	5.2-5.5	7						
2	Manubrium width	50	0.7	2.1	1.5	.047	.33	1.4-1.6	22	.232					
3	Manubrium length	50	0.7	2.6	1.6	0.69	.49	1.5-1.8	30	.461	.490				
4	Free prox. length	50	1.0	2.3	1.5	.046	.33	1.4-1.6	22	.225	.288	-.136			
5	Stipe divergence	50	280	360	321	3.4	24	314-328	7	-.145	-.664	-.532	-.279		
6	Prox. stipe width	50	1.4	3.0	2.0	.054	.38	1.9-2.2	19	.213	-.595	-.401	-.290	.721	
7	Distal stipe width	50	1.9	3.3	2.4	.049	.34	2.3-2.5	14	.236	-.600	-.328	-.403	.696	.880

Pseudisograptus manubriatus manubriatus

		N.	Min.	Max.	Mean	s_x	s	95% C.l.	V	1	2	3	4	5	6
1	Sicular length	12	4.3	5.9	4.8	.14	.50	4.5-5.0	10						
2	Manubrium width	13	1.7	2.4	1.9	.09	.33	1.7-2.1	17	-.179					
3	Manubrium length	13	0.5	0.9	0.7	.05	.19	.56-.79	27	.425	-.470				
4	Free prox. length	12	0.8	2.0	1.2	.10	.34	1.0-1.4	28	.768	.371	-.057			
5	Stipe divergence	13	310	335	320	4	14	312-329	4	-.451	-.188	-.579	-.112		
6	Prox. stipe width	13	2.2	3.2	2.6	.09	.32	2.4-2.8	12	.189	.425	-.633	.484	.602	
7	Distal stipe width	8	2.5	3.8	3.1	.2	.4	2.7-3.4	13	.500	.459	-.633	.651	.687	.382